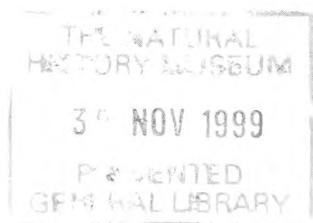


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Systematics and phylogeny of *Zausodes* C.B. Wilson, 1932 (Copepoda, Harpacticoida, Harpacticidae), including three new species from the northern Gulf of Mexico

LORI BOUCK

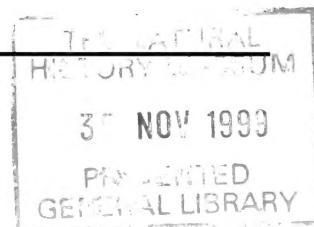
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SYNOPSIS. Re-examination of copepod material, collected from the northern Gulf of Mexico and previously identified as *Zausodes arenicolus* C.B. Wilson, 1932 (Harpacticoida, Harpacticidae), resulted in the discovery of three new species of the *Zausodes* complex. Phylogenetic analysis identified four distinct lineages within this complex which are attributed generic status. *Zausodes* C.B. Wilson, 1932 is redefined to include only *Z. septimus* Lang and the type species *Z. arenicolus* which is completely redescribed. A new genus *Mucropedia* is proposed to accommodate two new species from the Gulf of Mexico, *M. kirstenae* and *M. cookorum*. *Z. biarticulatus* Itô, 1979 from the Japanese Bonin Islands is transferred to *Archizausodes* gen. nov. and regarded as the most primitive member of the *Zausodes* complex. All other species are grouped in *Neozausodes* gen. nov., including *N. shulenbergeri* sp. nov. from the Gulf of Mexico and *N. areolatus* (Geddes, 1968a) comb. nov. which is completely redescribed on the basis of type material. *Z. cinctus* Krishnaswamy, 1954 is ranked *species incertae sedis* in the family Harpacticidae. The sister group relationship between *Perissocope* Brady, 1910 and the *Zausodes* complex is discussed. Lang's (1944, 1948) subfamilial division of the Harpacticidae is abandoned.

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INTRODUCTION

Species of *Zausodes* C.B. Wilson are typical inhabitants of sandy substrata in shallow subtidal localities, however, some records indicate that their horizontal zonation extends into the infralittoral of sandy beaches (Wilson, 1932; Mielke, 1990, 1997). Although the genus was originally proposed for the type species *Z. arenicolus* from the Woods Hole area (Wilson, 1932), most species that have been added since are subtropical in distribution. The genus currently comprises nine species but only two of them, *Z. arenicolus* and *Z. septimus* Lang, 1965, have been recorded again since their original description (Bell & Woodin, 1984; Coull, 1971a–b; Foy & Thistle, 1991; Mielke, 1990, 1997). The taxonomy and phylogenetic position of the genus within the family Harpacticidae are not well understood for a variety of reasons. First, species of *Zausodes* are amongst the smallest Harpacticidae and males often do not exceed 0.4 mm in size. Second, Wilson's (1932) generic diagnosis contains a number of significant inconsistencies which originate from his imperfect description of *Z. arenicolus*. Lang (1965) clarified some of the erroneous statements but did not present a complete redescription. Third, several subsequent descriptions are grossly inadequate and severely hamper both species identification and phylogenetic reconstruction of relationships. This is particularly the case for the species described by Jakobi (1954) and Krishnaswamy (1954). Finally, the current subfamilial classification of the Harpacticidae introduced by Lang (1948) is inadequate. The genus *Zausodes* was placed in the Zausodiinae together with *Zaus* Goodsir and *Zausopsis* Lang, however recent discoveries of new taxa (Itô, 1979; Watkins, 1987) have provided strong indications for a close relationship between *Zausodes* and *Perissoscope* Brady, a genus currently assigned to the Harpacticinae.

While examining a collection of harpacticoids from the northern Gulf of Mexico, previously identified by D.Thistle and co-workers as *Z. arenicolus* (Foy & Thistle, 1991; Ravenel & Thistle, 1981; Thistle, 1980; Thistle *et al.*, 1995), we found several other species of *Zausodes* which could not be assigned to the type species. Although *Z. arenicolus* was present among the specimens, as confirmed by comparison with Wilson's type material, three species new to science were found. Since one of these was very similar to *Z. areolatus* Geddes, the type locality of which is in the relatively nearby Caribbean (Geddes, 1968a), the type material of the latter was obtained for comparison.

This paper describes the three new species from the Gulf of Mexico, provides complete redescriptions for both *Z. arenicolus* and *Z. areolatus* and analyses the phylogenetic relationships between the species. The genus *Zausodes* is redefined in the light of these findings.

MATERIALS AND METHODS

Samples were taken by SCUBA divers with a 15.5 cm² corer. The top 3 cm of each core were preserved in sodium-borate-buffered formalin. In the laboratory, harpacticoids were concentrated from each sample with a modified Barnett (1968) extraction technique combined with a 0.062-mm mesh sieve. After rose bengal staining, harpacticoids were sorted under a dissecting microscope and mounted in glycerol on slides.

Specimens were dissected in lactic acid, and the dissected parts were placed in Hoyer's mounting medium (Pfannkuche & Thiel, 1988) on H-S mounts (Shirayama *et al.*, 1993) or Cobb slide frames

(Westheide & Purschke, 1988). Drawings were prepared with a camera lucida on a Zeiss Standard 16 compound microscope equipped with differential interference contrast. Habitus views were drawn at 800×; other illustrations were drawn at 2000×. Body size was measured along a line halfway between the dorsal and ventral margins in lateral view at 256× with the aid of a camera lucida. Terminology follows Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae = aesthetasc; P1–P6 = first to sixth thoracopods; exp(enp)–1(2,3) to denote the proximal (middle, distal) segment of a ramus.

Phylogenetic relationships between taxa were analyzed using the phylogenetic computer package PAUP 3.1 prepared by David L. Swofford of the Laboratory of Molecular Systematics, Smithsonian Institution (Swofford, 1993; Swofford & Begle, 1993). Since evolution within the Copepoda is assumed to proceed typically by oligomerization (Huys & Boxshall, 1991), all characters were set irreversible using the CAMIN–SOKAL option. This option suppresses character reversals at the expense of introducing extra convergences and thereby increasing the tree-length. The options employed in the analysis were BRANCH AND BOUND, which guaranteed to find all most parsimonious trees, and the MINF optimization, which assigns character states so that the f-value is minimized.

SYSTEMATICS

For practical reasons the systematics section of this paper is arranged according to the conclusions arrived at in the phylogeny section below. Species are allocated to genera following the topology of the most parsimonious cladogram obtained by the phylogenetic analysis (Fig. 33A).

Family Harpacticidae Dana, 1846

Genus *Zausodes* C.B. Wilson, 1932

In its revised concept (see below) the genus is restricted here to the type species and *Z. septimus*. Lang (1965) had already recognized the close relationship between these species, pointing out their similarity in the ♀ P5. *Z. arenicolus* displays two characters which are not found in any of the species of the former *Zausodes* complex: (1) the 3-segmented P4 endopod, and (2) the presence of a mucroniform process on enp-2 of the male P2. The former is an evolutionary labile character, frequently showing intermediate states in other species (Lang, 1965), whilst the latter is regarded here as a plesiomorphy retained within the former *Zausodes* complex only in *Z. arenicolus*, but being present in many other harpacticid genera such as *Perissoscope*, *Harpacticus* Milne-Edwards and *Tigriopus* Norman (Huys *et al.*, 1996). It is assumed that in all other species of the former *Zausodes* complex this process was secondarily lost.

DIAGNOSIS. Harpacticidae. Antennule ♀ 8-segmented, with pinnate or plumose setae on segments 1–6; without strong, modified spines on segments 3–5 or enlarged pectinate or pinnate spines on segment 6. Antennule ♂ without modified spines on segment 3. Antennary exopod 1-segmented, with 2 apical setae. Maxilla with 4 spines/setae on praecoxal endite. P2–P3 endopods 3-segmented, P4 endopod 2- or 3-segmented. P2 ♀ enp-3 with 2 inner setae. P3 ♀ enp-2 without inner seta. P4 exp-3 with 3 outer spines in both sexes. P4 enp-3 (or enp-2 when 2-segmented) with 1 inner seta in both sexes.

P2♂enp-2 with or without apophysis, inner seta not modified; enp-3 with 1 apical seta (inner one lost), outer spine not fused to segment. P3♂enp-2 outer distal corner not attenuated.

Swimming leg setal formula:

	exopod	endopod
P2	0.1.223	0.1.221 [♀] 0.1.211 [♂]
P3	0.1.323	1.0.221
P4	0.1.323	1.0.121 or 1.121

P5 exopod elongate-oval in both sexes. P5 endopodal lobe ♀ expressed; 3rd and 4th inner setae much shorter than others (or 1 seta lost in *Z. septimus*).

Sexual dimorphism in rostrum, antennule, P2 endopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Zausodes arenicolus* C.B. Wilson, 1932 (by monotypy).

OTHER SPECIES. *Z. septimus* Lang, 1965.

Zausodes arenicolus C.B. Wilson, 1932

TYPE LOCALITY. Katama Bay, Martha's Vineyard, Woods Hole (Massachusetts); beach sand washings.

MATERIAL EXAMINED.

National Museum of Natural History (Smithsonian Institution), Washington, D.C.: Woods Hole region; type series consisting of one vial containing >50 specimens (USNM 63877); 1 ♀ and 1 ♂ dissected for examination. According to the USNM catalogue files the holotype ♂ has gone missing since at least 1983 when the harpacticoid collections were inventoried. It is assumed that in reality the holotype was never segregated by C.B. Wilson although the empty vial, which supposedly contained the specimen, received a separate registration number (no. 63423).

The Natural History Museum, London: syntypes (4 ♀ ♀, 4 ♂ ♂) in alcohol; from type locality; coll. C.B. Wilson, 15 August 1927; BMNH 1948.9.10.37.

Gulf of Mexico: 29°51'N, 84°31'W (about 50 m north of day mark #2), St. George Sound, Florida, 5 m depth, unvegetated medium sand (median grain size = 0.254 mm); a seagrass meadow occurs about 150 m to the north; see Foy & Thistle (1991) for additional description. Deposited at the Natural History Museum, London are 9 ♀ ♀ and 3 ♂ ♂ in ethanol (BMNH 1999.176–187) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.188–191). Deposited at the Smithsonian, Washington, D.C. are 9 ♀ ♀ and 2 ♂ ♂ in ethanol (USNM 288445–446) and 1 ♀ ♀ and 2 ♂ ♂ dissected on slides (USNM 288444).

REDESCRIPTION. All illustrations and text are based on specimens from the Gulf of Mexico. Illustrations were compared to type material obtained from the Smithsonian in order to verify the species identification.

FEMALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 433 µm ($\bar{x} = 0.499$, n = 4); without rostrum and caudal rami: 394 µm ($\bar{x} = 0.456$, n = 4). Body (Figs 1A–B, 2C–D) dorsoventrally flattened. Greatest width 200 µm ($\bar{x} = 0.202$, n = 4), measured near posterior margin of cephalothorax. Nauplius eye distinct; reddish brown in fresh, unstained specimens; invisible in cleared specimens. Integument with surface ornamentation/sculpturing consisting of irregular pattern of fine striations (not illustrated). Sensillae present dorsally and dorsolaterally on cephalothorax and body somites except penultimate one (not all

shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of thoracic somites thickly chitinized laterally. All somites but anal with fine spinular rows dorsally and dorsolaterally; penultimate somite with ventral spinular row; anal somite with spinular rows dorsally, ventrally, and laterally on the posterior margin. Lateral margins of free thoracic somites with 3 sensillae. Ventral posterolateral corners of urosomites 3–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is partially exposed in dorsal aspect; with two ventral pores near posterior margin; anal operculum rounded, smooth; pseudoperculum present, weakly developed. Caudal rami (Figs 1A–B, 2C–D) approximately as long as wide, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string (Figs 1A–B) extending posteriorly from each caudal ramus present in some specimens.

Rostrum (Fig. 1C) prominent, bell-shaped in dorsal view, with membranous fringe, defined at base; with two short sensillae anteriorly and one sensilla on each mediolateral margin; with mid-dorsal pore.

Antennule (Fig. 2B) 8-segmented; segments 2 and 3 longest; first segment widest with several spinular rows; fourth segment with an aesthetasc (50 µm long); eighth segment with acrothek consisting of 3 elements (probably 2 setae and 1 aesthetasc, however, we were unable to distinguish which elements were setae and which was an aesthetasc); with armature formula 1-[1], 2-[9 + 1 pinnate], 3-[7 + 2 pinnate], 4-[3 + 1 pinnate + (1 + ae)], 5-[1 + 1 pinnate], 6-[2 + 2 pinnate], 7-[4], 8-[4 + acrothek].

Antenna (Fig. 2A). Coxa short and unornamented; allobasis with several spinular rows, abexopodal spinulose seta, and membranous insert marking original segment boundary between basis and first endopodal segment; free endopod 1-segmented; lateral armature consisting of a spine, 1 short seta and 1 long seta; distal armature comprising 1 seta, 1 pinnate, curved spine, and 4 geniculate spines, longest one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinular rows and hyaline surface frill as indicated in Fig. 2A; exopod 1-segmented with 2 distal, unequal setae.

Labrum well developed, medially incised.

Mandible (Fig. 3A). Gnathobase with seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod longer than exopod, with 1 bare and 1 pinnate lateral seta and 6 apical setae; exopod with 1 pinnate and 2 bare lateral setae, 3 distal setae, and spinules subdistally and along outer margin.

Maxillule (Fig. 3C). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 4 setae and a spinular row; basal endite with 6 setae; endopod with 1 bare and 2 pinnate setae distally; exopod with 1 bare inner seta, 1 pinnate outer seta, 2 distal setae, and a spinular row.

Maxilla (Fig. 3B). Syncoxa with spinular row along outer margin and 3 endites; praecoxal endite with 2 bare and 2 bipinnate setae; coxal endites each with 2 bare setae and 1 pinnate spine; allobasis with claw and 3 bare setae; endopod 1-segmented with 4 bare setae.

Maxilliped (Fig. 3D). Syncoxa with a bipinnate seta and numerous spinular rows as indicated; basis with a spinular row and seta along palmar margin, with spinules along outer distal margin and on anterior face; endopod represented by acutely recurved claw with spinules along inner margin and proximal accessory seta.

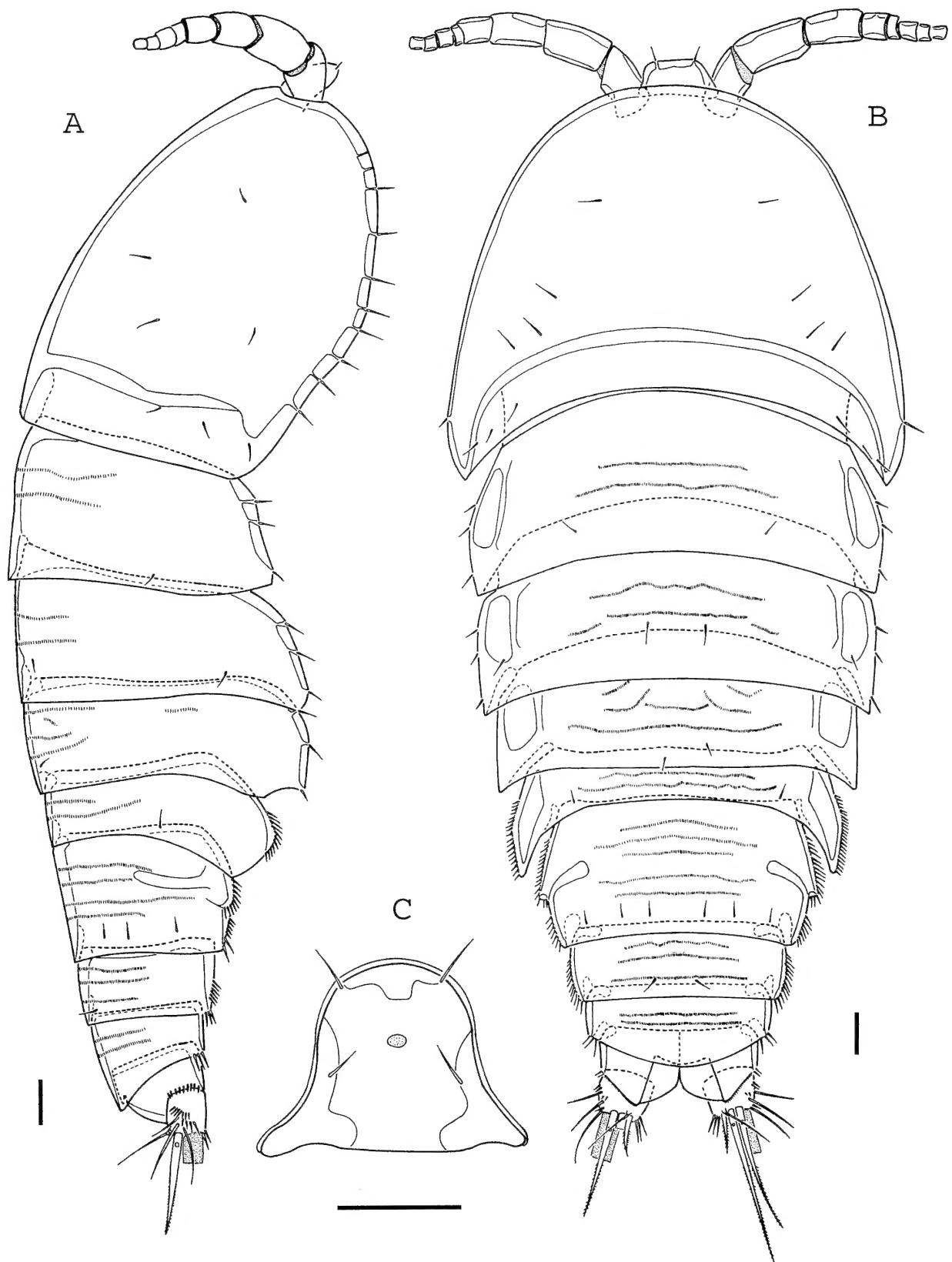


Fig. 1 *Zausodes areniculus* C.B. Wilson, 1932 (♀). A, Habitus, lateral view; B, habitus, dorsal view; C, rostrum. Scale bars = 20 µm.

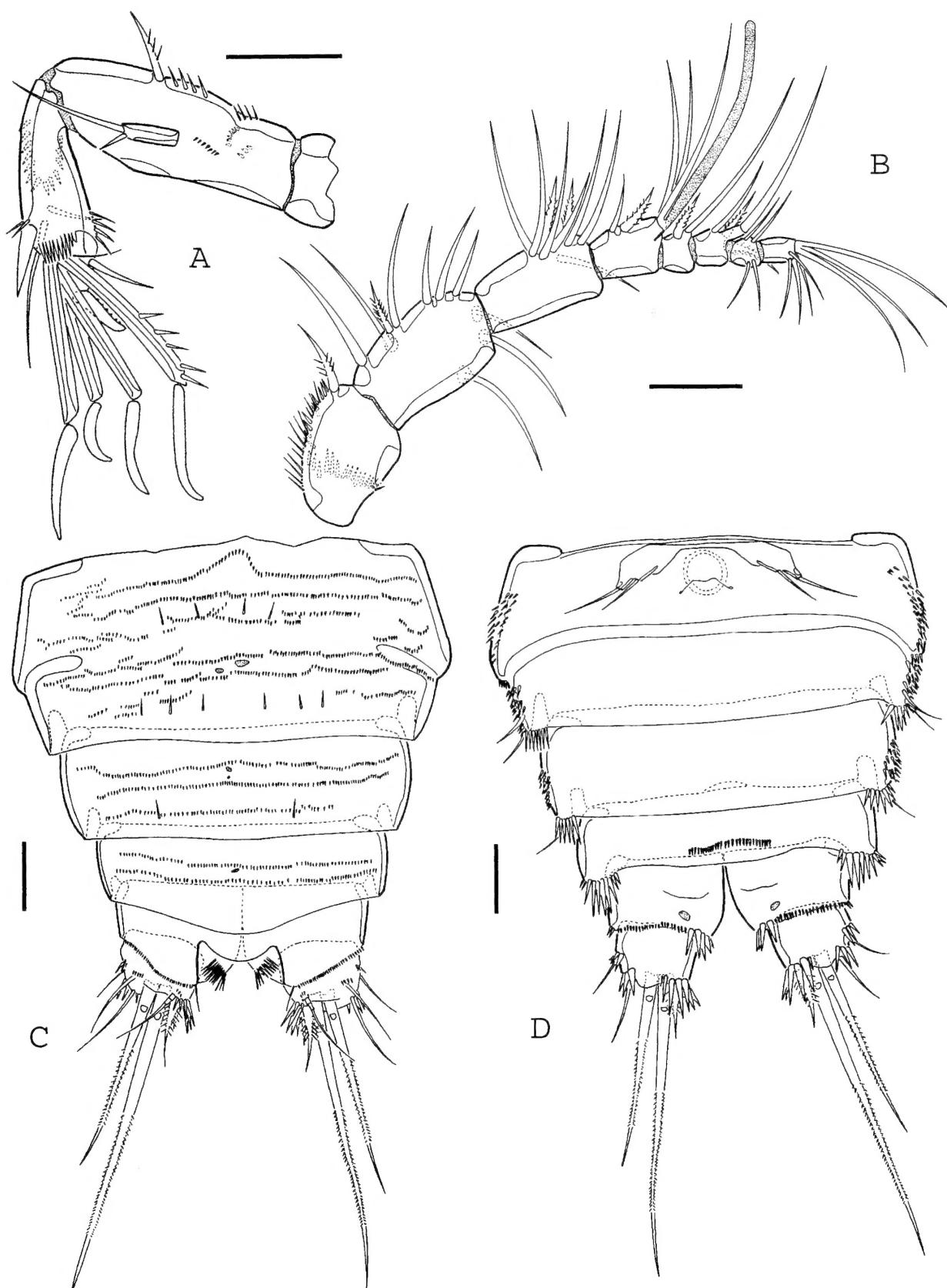


Fig. 2 *Zausodes arenicola* C.B. Wilson, 1932 (♀). A, Antenna; B, antennule; C, urosome (excluding P5-bearing somite), dorsal view; D, urosome (excluding P5-bearing somite), ventral view; Scale bars = 20 µm.

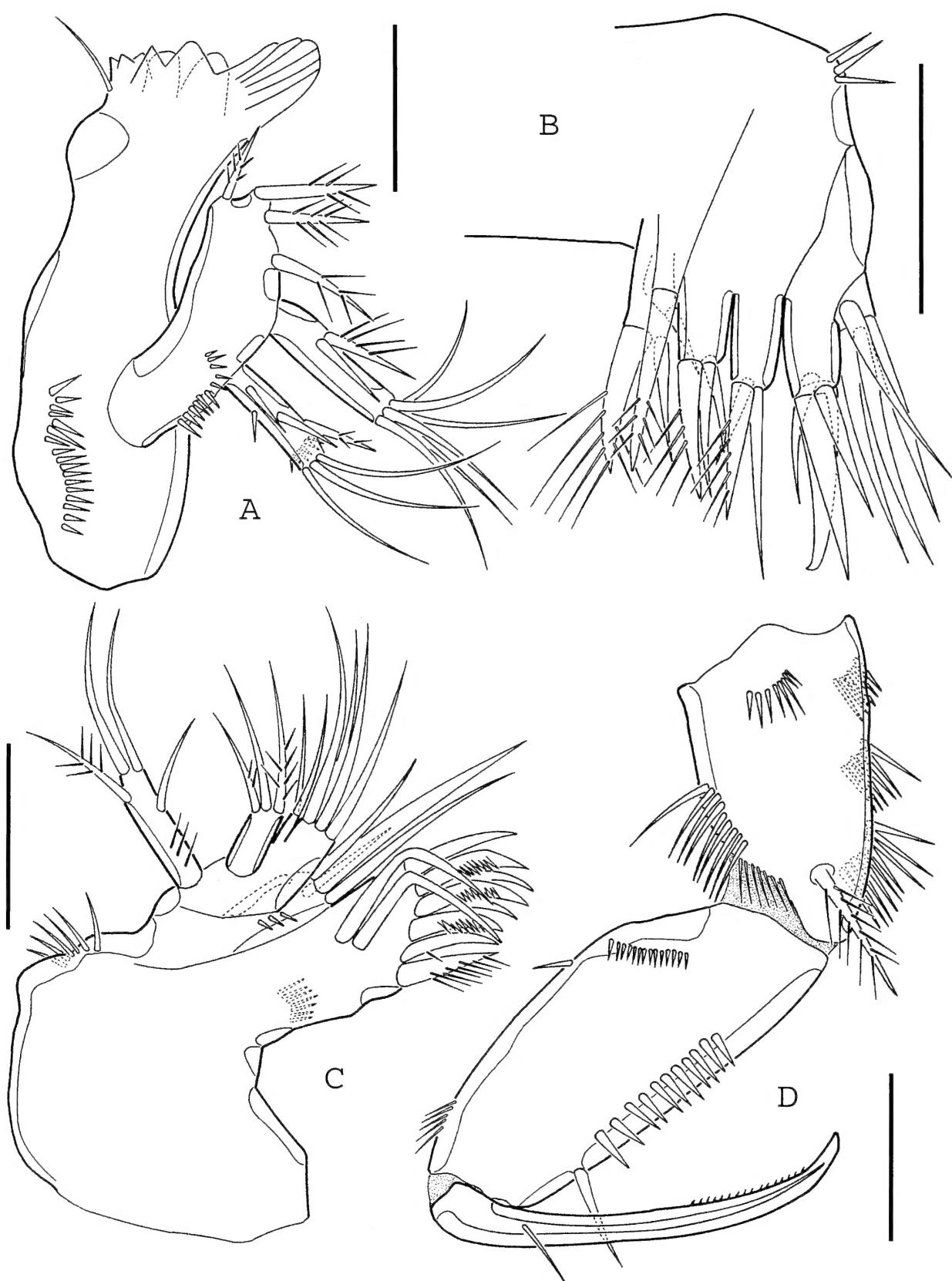


Fig. 3 *Zausodes areniculus* C.B. Wilson, 1932 (♀). A, Mandible; B, maxilla; C, maxillule; D, maxilliped. Scale bars = 20 µm.

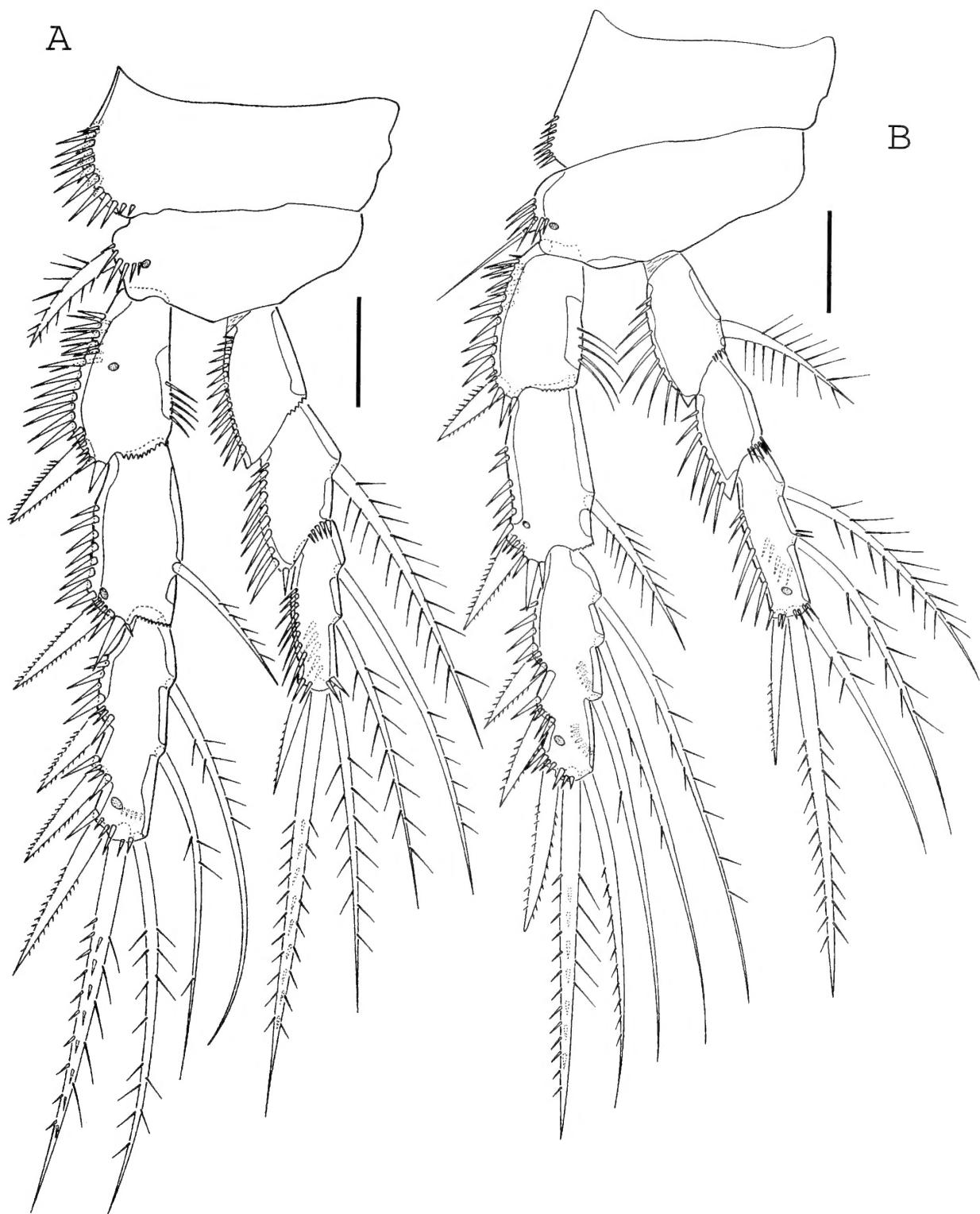


Fig. 4 *Zausodes areniculus* C.B. Wilson, 1932 (♀). A, P2; B, P3. Scale bars = 20 µm.

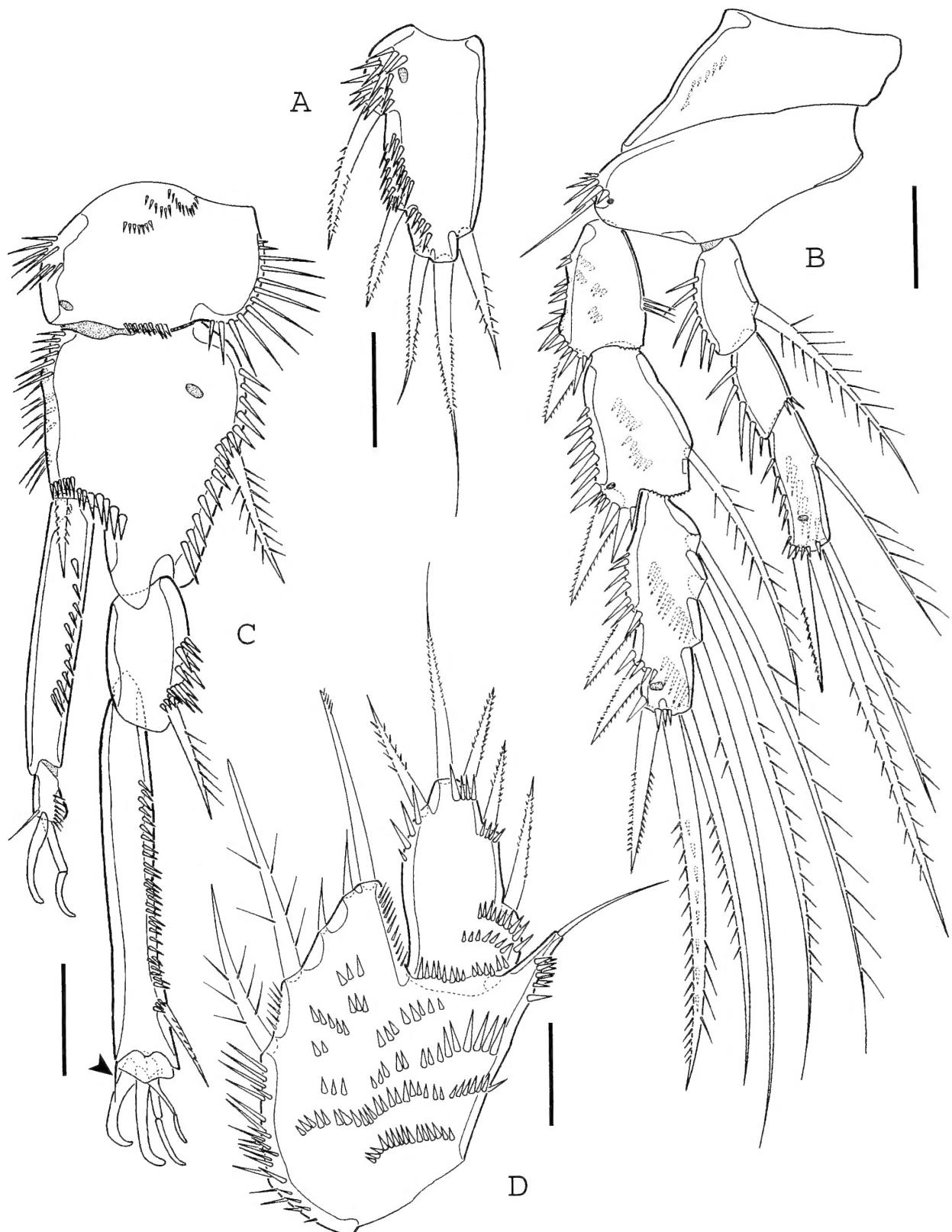


Fig. 5 *Zausodes areniculus* C.B. Wilson, 1932 (♀). A, P5 exopod, posterior view; B, P4; C, P1 (arrow indicating rudimentary seta); D, P5, anterior view.
Scale bars = 20 µm.

P1 (Fig. 5C). Rami prehensile; coxa with spinular rows along inner, outer, and distal margins and on anterior face, with pore at inner distal corner; basis with bipinnate seta near mid-point of outer margin and bipinnate spine at inner distal corner; spinular rows present along inner and outer margins and around articulation with endopod; with pore near outer proximal corner. Exopod 3-segmented, 1.5 times as long as endopod (excluding apical elements); exp-1 with distal pinnate seta and spinular rows along outer margin; exp-2 elongate, 2.6 times as long as exp-1, with short, slender inner seta distally (arrowed) and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate, with outer spinular row; enp-2 0.2 times as long as exp-1, with outer spinular row and bearing geniculate spine, claw, and short, slender inner seta distally.

P2–P4 (Figs 4A–B, 5B) with 3-segmented rami. Coxae with spinular rows at outer distal corner of P2–P3 and posteriorly near outer edge of P4. Bases with outer bipinnate spine (P2) or naked seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P2–P4 exp-3, P4 exp-1 and -2, P2–P4 enp-3. Outer distal spine of P2–P4 exp-3 and P2 enp-3 tripinnate. Pores present as illustrated (Figs 4A–B, 5B). Seta and spine formula of P2–P4 as in Table 1.

P5 (Figs 5A,D) biramous, not fused medially. Baseoendopod with numerous anterior surface and marginal spinular rows; endopodal lobe triangular, with 2 sparsely plumose and 2 short bare setae along inner margin and 1 distally pinnate seta apically; outer basal seta slender and arising from cylindrical process. Exopod 1.9 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer bipinnate spines, apical one with flagellate tip; posterior surface with proximal pore near outer margin.

Genital double somite (Figs 2C–D) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 2 naked setae.

MALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 366 µm ($\bar{x} = 0.379 \mu\text{m}$, $n = 4$); without rostrum and caudal rami: 294 µm ($\bar{x} = 338 \mu\text{m}$, $n = 4$). Body width 147 µm ($\bar{x} = 149 \mu\text{m}$, $n = 4$). Not all sensillae shown in habitus views (Figs 6A–B). Sexual dimorphism in body size, rostrum, antennule, P2 endopod, P5, P6, and urosome segmentation (Figs 7A–B).

Rostrum (Fig. 6A) trapezoid, defined at base.

Antennule (Figs 6C–D) 6-segmented, chirocer; segment 5 bearing aesthetasc, not conspicuously swollen; segments 3 and 5 longest; with geniculation between segments 5 and 6; first segment with several spinular rows along anterior margin; with armature formula 1–[1], 2–[1], 3–[9], 4–[10], 5–[6 + (1 + ae)], 6–[6 + acrothek].

P2 (Fig. 7E) as in ♀ except for endopod. Enp-1 with outer row of spinules. Enp-2 with outer distal corner produced into spinous apophysis, extending to distal margin of enp-3; outer margin spinulose; inner margin with subdistal bipinnate seta. Enp-3 with spinulose outer margin, short outer pinnate spine, long bipinnate spine distally and 2 pinnate inner setae; with spinules on posterior face and at bases of distal inner and apical elements.

P5 (Figs 7C–D) biramous. Baseoendopods fused medially forming transversely elongate plate; endopodal lobe slightly developed, with 1 outer, distally pinnate seta and 1 inner, bipinnate seta; outer basal seta slender and arising from cylindrical process; with spinules

around articulation with exopods. Exopod as in ♀ except for an additional small, bipinnate seta along the outer margin, and fewer spinular rows.

P6 (Fig. 7B) symmetrical; with distal seta and spinules along outer margin; located more laterally than in ♀.

NOTES.

Wilson (1932) noted sexual dimorphism in the first pair of swimming legs and the exopods of P3–P4 and further claimed that none of the other rami was genuinely modified in the male. Lang (1965) re-examined type specimens of *Z. arenicolus* and concluded that neither P1 nor P3–P4 displayed sexual dimorphism and that Wilson had overlooked the modification of the male P2 endopod.

Coull's (1971b) numerous records from the North Carolina shelf, Bell & Woodin's (1984) record from Virginia, Bell's records from Tampa Bay (e.g. Bell *et al.*, 1989), and this paper suggest that *Z. arenicolus* assumes a continuous distribution along the American east coast from Massachusetts, around the Florida peninsula, and into the northern Gulf of Mexico.

Zausodes septimus Lang, 1965

TYPE LOCALITY. California, Monterey Bay, off Hopkins Marine Station, about 7 m depth.

NOTES.

The few disjunct records of this species suggest a wide distribution both in the Caribbean and along the Pacific seaboard of the U.S. and Latin America. Mielke (1990) found *Z. septimus* along both Pacific and Caribbean coasts of Panamá and subsequently recorded the species also from Punta Morales in Costa Rica (Mielke, 1997). Coull (1971a) identified *Z. septimus* from sediment samples taken on St. Thomas (U.S. Virgin Islands).

Mielke's (1990) specimens from Panamá (particularly from the Caribbean side; Isla Nalunega) are remarkably smaller than those from the type locality in California but otherwise agree in most aspects with Lang's (1965) description. Significant discrepancies are found in (1) the shape of the rostrum which is squarish and truncate in the Californian material but elongate bell-shaped and pointed in Mielke's material, (2) the proportional lengths of the antennular segments in the ♀ (particularly segments 3–4 are distinctly shorter in the Panamá females), (3) the length of P1 endopod which is markedly shorter in Lang's specimens, and (4) the shape and length of outer and apical spines of P2–P4 exp-3 which are stouter and shorter in the Panamá population. A further study based on material from a wider range of localities is required to confirm whether these differences originate from intraspecific variability as Mielke (1990, 1997) advocates, or reflect the existence of two closely related species.

Z. septimus can be differentiated from *Z. arenicolus* by the segmentation of the P4 endopod and by the shape of the P5 baseoendopod and the relative position of its setae. Males of both species can be distinguished by their P2 endopod (i.e. enp-2 with mucroniform process in *Z. arenicolus*).

Genus *Neozausodes* gen. nov.

Lang (1965) remarked on the close similarity between *Z. sextus* and the three Brazilian species *Z. limigenus*, *Z. stammeri* and *Z. paranaguaensis*. Geddes (1968a) regarded *Z. areolatus* as morphologically closest to *Z. sextus*. As a result of the phylogenetic analysis these 5 species together with *N. shulenbergeri* sp. nov. are grouped here in a new genus.

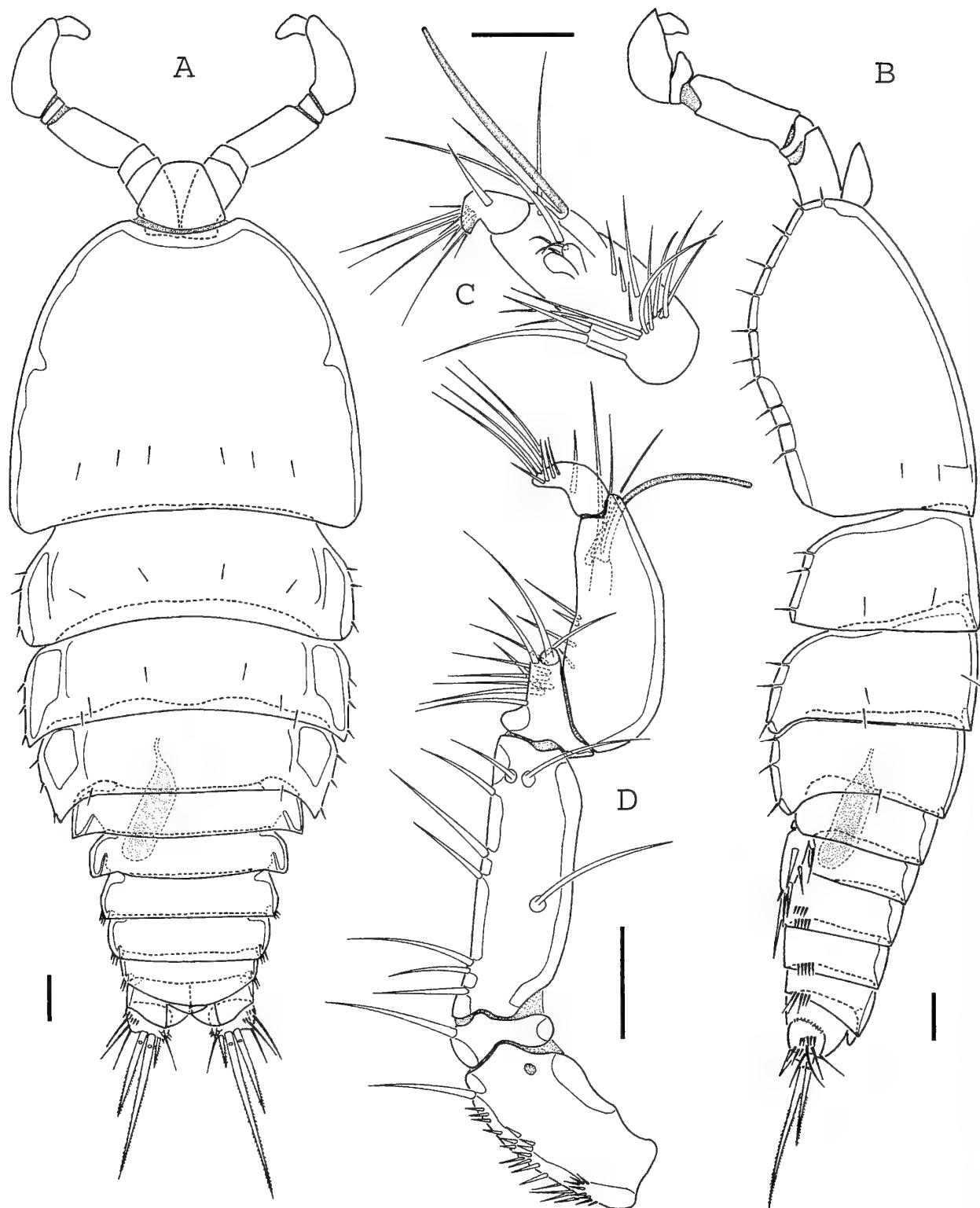


Fig. 6 *Zausodes areniculus* C.B. Wilson, 1932 (♂). A, Habitus, dorsal view; B, habitus, lateral view; C, antennule, fifth and sixth segments, anterior view; D, antennule, dorsal view. Scale bars = 20 µm.

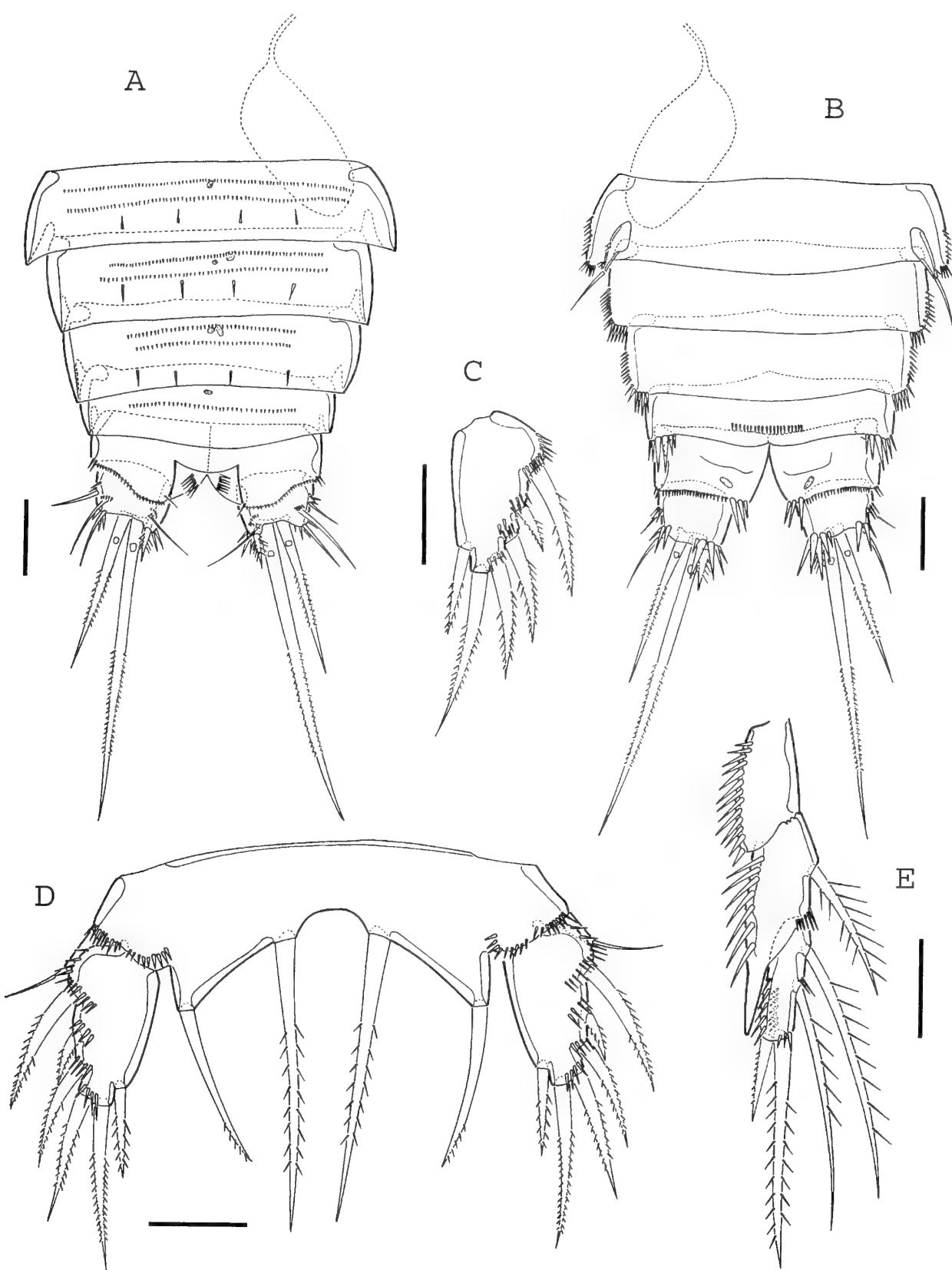


Fig. 7 *Zausodes areniculus* C.B. Wilson, 1932 (σ^{\prime}). A, Urosome, dorsal view; B, urosome, ventral view; C, P5 exopod, posterior view; D, P5, anterior view; E, P2 endopod. Scale bars = 20 μm .

DIAGNOSIS. Harpacticidae. Antennule ♀ 6- or 7-segmented, without pinnate or plumose setae on segments 1-6; with strong, modified spines on segments 3-5 and enlarged pectinate or pinnate spines on segment 6. Antennule ♂ with modified spine on segment 3. Antennary exopod 1-segmented, with 2 apical setae. Maxilla with 3 spines/setae on praecoxal endite. P2 endopod 3-segmented (2- in ♂ of *N. areolatus*), P3 endopod 2- or 3-segmented, P4 endopod 2-segmented. P2 ♀ enp-3 with 1-2 inner setae. P3 ♀ enp-2 without inner seta. P4 exp-3 with 3 outer spines in both sexes. P4 enp-2 with 1 inner seta in both sexes. P2 ♂ enp-2 without apophysis, inner seta (proximal one in 2-segmented endopod of *N. areolatus*) not modified; enp-3 (-2 in *N. areolatus*) with 1 apical seta (inner one lost), outer spine not fused to segment. P3 ♂ enp-2 outer distal corner not attenuated.

Swimming leg setal formula:

	exopod	endopod	
P2	0.1.223	0.1.221 or 0.1.121	[♀]
		0.1.211	[♂ <i>sextus</i>]
		0.311	[♂ <i>areolatus</i>]
		0.1.111	[♂ other species]
P3	0.1.323	1.0.221 or 1.221	
P4	0.1.323	1.121	

P5 exopod round in both sexes. P5 endopodal lobe ♀ expressed; all setae well developed.

Sexual dimorphism in rostrum, antennule, P2 endopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Zausodes areolatus* Geddes, 1968a = *Neozausodes areolatus* (Geddes, 1968a) comb. nov.

OTHER SPECIES. *Z. limigenus* Jakobi, 1954 = *N. limigenus* (Jakobi, 1954) comb. nov.; *Z. paranaguaensis* Jakobi, 1954 = *N. paranaguaensis* (Jakobi, 1954) comb. nov.; *Z. stammeri* Jakobi, 1954 = *N. stammeri* (Jakobi, 1954); *Z. sextus* Lang, 1965 = *N. sextus* (Lang, 1965) comb. nov.; *N. shulenbergi* sp. nov.

ETYMOLOGY. The generic name is derived from the Greek prefix *neos*, meaning new, and alludes to the advanced position of this genus within the *Zausodes*-group. Gender: masculine.

Neozausodes areolatus (Geddes, 1968a) comb. nov.

TYPE LOCALITY. Bahamas, Eleuthera, SW of Glass Window; 25°26'03"N, 76°36'10"W; 5 m depth, sand bottom.

MATERIAL EXAMINED.

American Museum of Natural History: holotype ♀ dissected and mounted on 3 slides (AMNH 12944); paratypes are 1 ♀ and 1 ♂ dissected on 3 slides each, and 8 ♀ in alcohol, collected from type locality (AMNH 12945). Note that the holotype registration number was inadvertently misprinted in Geddes (1968a) as 12949.

Zoological Museum of the University of Bergen: paratypes (2♂♂, 3♀♀) from Exuma Cays, Great Guana Cay, between White Point and Black Point, 24°04'25"N, 76°23'45"W; 3-4 m depth, sand bottom (ZMUB 49315).

REDESCRIPTION. All female illustrations are from the holotype except Figs 8B-C, which are from paratypes. Male habitus and P5 illustrations are from a Bergen Museum paratype; other male illustrations are from an AMNH paratype.

FEMALE. Body length measurements from AMNH paratypes: measured from anterior margin of rostrum to posterior margin of caudal rami: $\bar{x} = 606 \mu\text{m}$ ($n = 3$); without rostrum and caudal rami:

$\bar{x} = 561 \mu\text{m}$ ($n = 3$). Body (Figs 8B-C, 9B-C) dorsoventrally flattened. Body width: $\bar{x} = 314 \mu\text{m}$ ($n = 3$). Integumental surface (e.g. A1, rostrum, urosome) with areolated ornamentation/sculpturing (not illustrated). Sensillae present dorsally and dorsolaterally on urosomites 2-4 and anal somite. Urosomites 2-5 with fine denticle rows dorsally and dorsolaterally; antepenultimate and penultimate somites with ventral spinular rows; anal somite with spinular rows dorsally, ventrally, and laterally on the posterior margin. Ventral posterolateral corners of urosomites 4-5 and lateral margins of urosomites 2-4 with spinules. Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is partially exposed in dorsal and ventral aspects; with two ventral pores near posterior margin; anal operculum and reduced pseudopericulum present. Caudal rami (Figs 8B-C, 9B-C) wider than long, with 7 setae: setae I-III bare, setae IV-V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. No gelatinous string was apparent.

Rostrum (Fig. 9A) prominent, lateral margins roughly parallel, defined at base; with two short sensillae anteriorly and two sensillae subdistally; with middorsal pore.

Antennule (Fig. 8A) 6-segmented; segments 1 and 2 longest; first segment widest with spinules; fourth segment with an aesthetasc (50 μm long), a surface indentation running from the anterior margin towards, but not reaching, the posterior margin, and an uninterrupted cuticle extending the length of the posterior margin; with setal formula 1-[1], 2-[10], 3-[8 + 2 unipinnate], 4-[4 + 2 unipinnate + (1 + ae)], 5-[6 + 2 pinnate], 6-[5 + acrothek]. The setal formula was based on the holotype, but setae missing in the holotype specimen that were found in the paratypic slides were added to the formula. Added setae include 1 seta from segment 2, 1 unipinnate seta from segment 3, and 1 seta from segment 5. The setation in the illustration is a composite, showing all setae.

Antenna (Fig. 9D). Coxa short and unornamented; allobasis with spinular row, abexopodal seta, and membranous insert marking original segment boundary between basis and first endopod segment; free endopod 1-segmented; lateral armature consisting of a pinnate spine and 1 pinnate, 1 short bare, and 1 long bare seta; distal armature comprising 1 seta, 1 unipinnate, curved spine, and 4 geniculate spines, longest one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinular rows and hyaline surface frill as indicated in Fig. 9D; exopod 1-segmented with 2 distal, unequal setae and a spinular row. The short, bare, lateral seta of the endopod was found on the paratype but could not be discerned on the holotype.

Mandible (Fig. 10A). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 3 bipinnate setae (one of which broken off in the holotype but observed in the paratype); endopod longer than exopod, with 1 bare and 1 pinnate lateral seta and 6 apical setae; exopod with 3 lateral and 4 distal setae and subdistal spinules.

Maxillule (Fig. 10C). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 5 setae; basal endite with 6 setae; endopod with 3 pinnate setae distally and a lateral spinular row; exopod with 1 pinnate inner seta, 1 bare and 2 pinnate distal setae.

Maxilla (Figs 10E-F). Syncoxa with 3 endites; praecoxal endite with 3 bipinnate setae; coxal endites each with 1 bare seta and 2 pinnate setae; allobasis with claw and 3 bare setae; endopod 1-segmented with 1 distally pinnate and 3 bare setae.

Maxilliped (Fig. 10D). Syncoxa with a pinnate seta and numerous

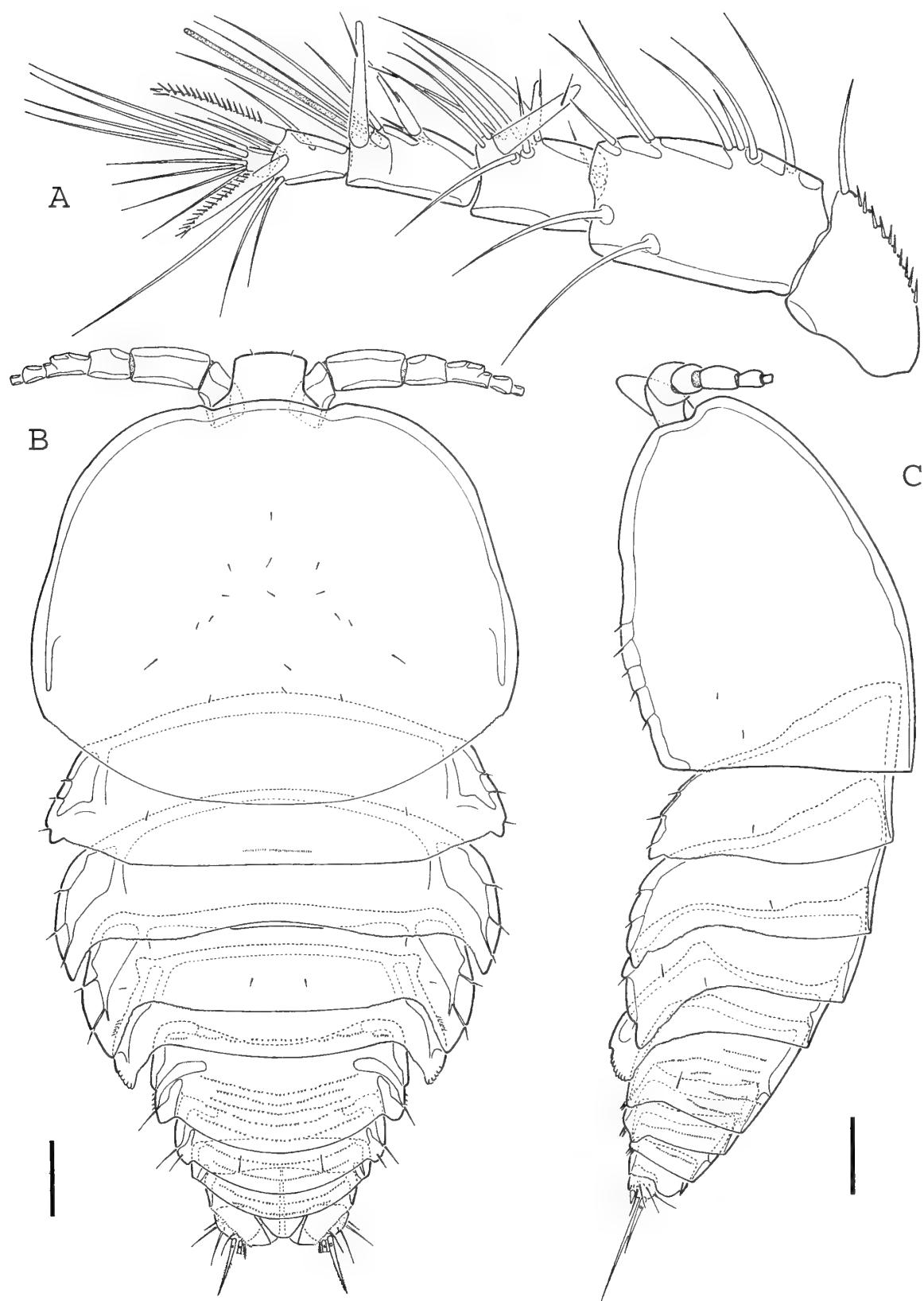


Fig. 8 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, Antennule; B, habitus, dorsal view (somewhat distorted); C, habitus, lateral view.
Scale bars = 50 µm.

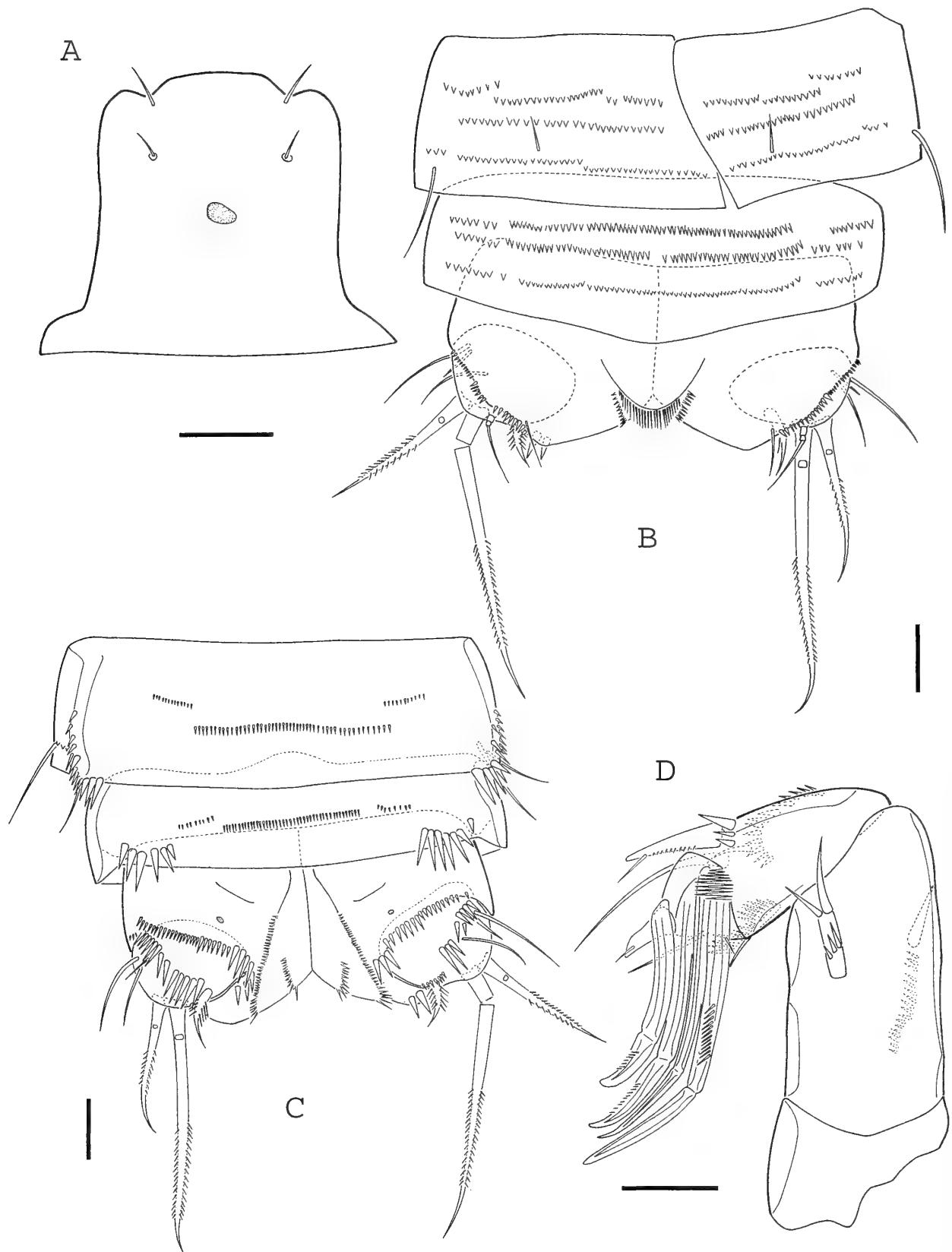


Fig. 9 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, Rostrum; B, last 3 urosomites and caudal rami, dorsal view; C, same, ventral view; D, antenna. Scale bars = 20 µm.

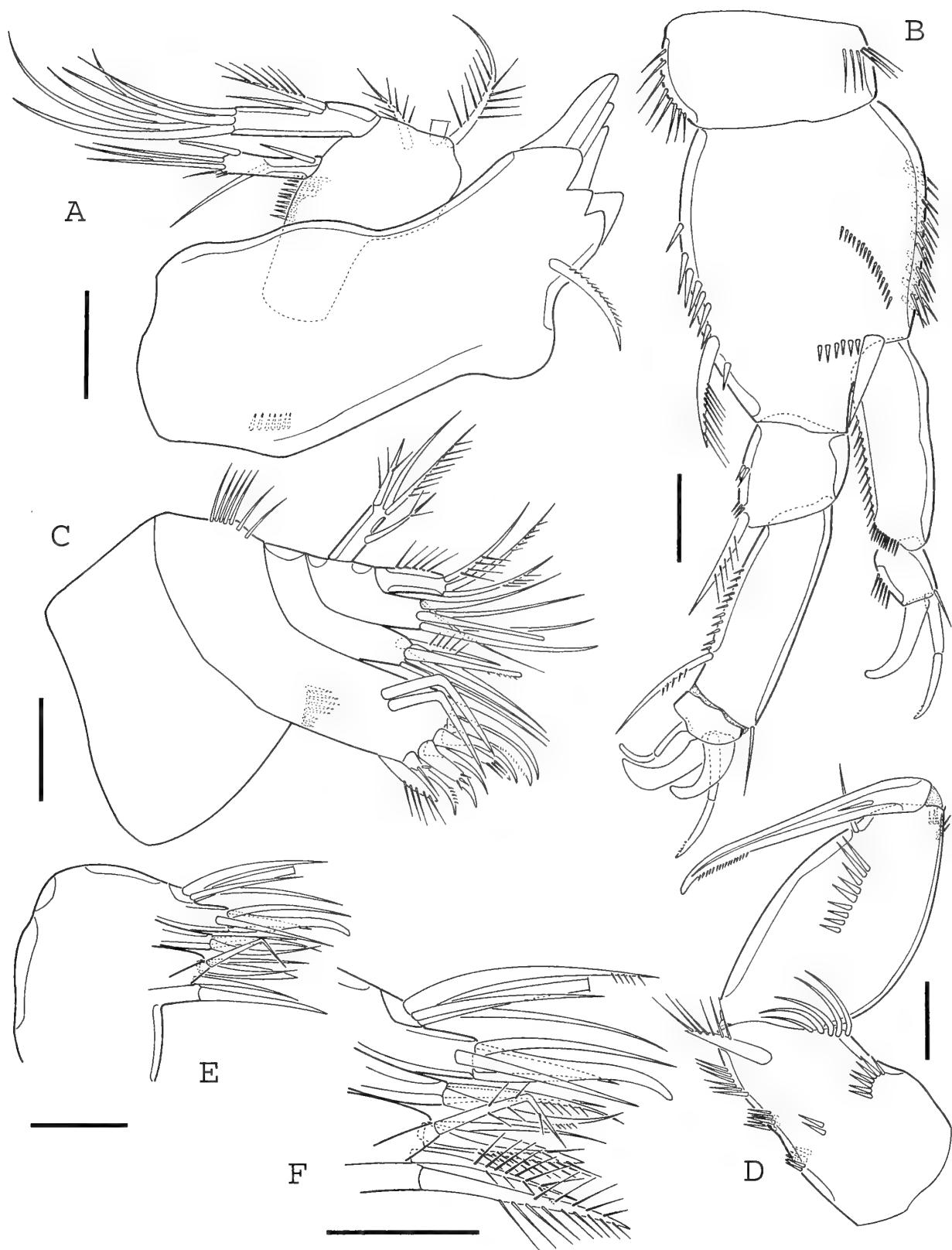


Fig. 10 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, Mandible; B, P1; C, maxillule; D, maxilliped; E, maxilla; F, maxillary endites. Scale bars = 20 µm.

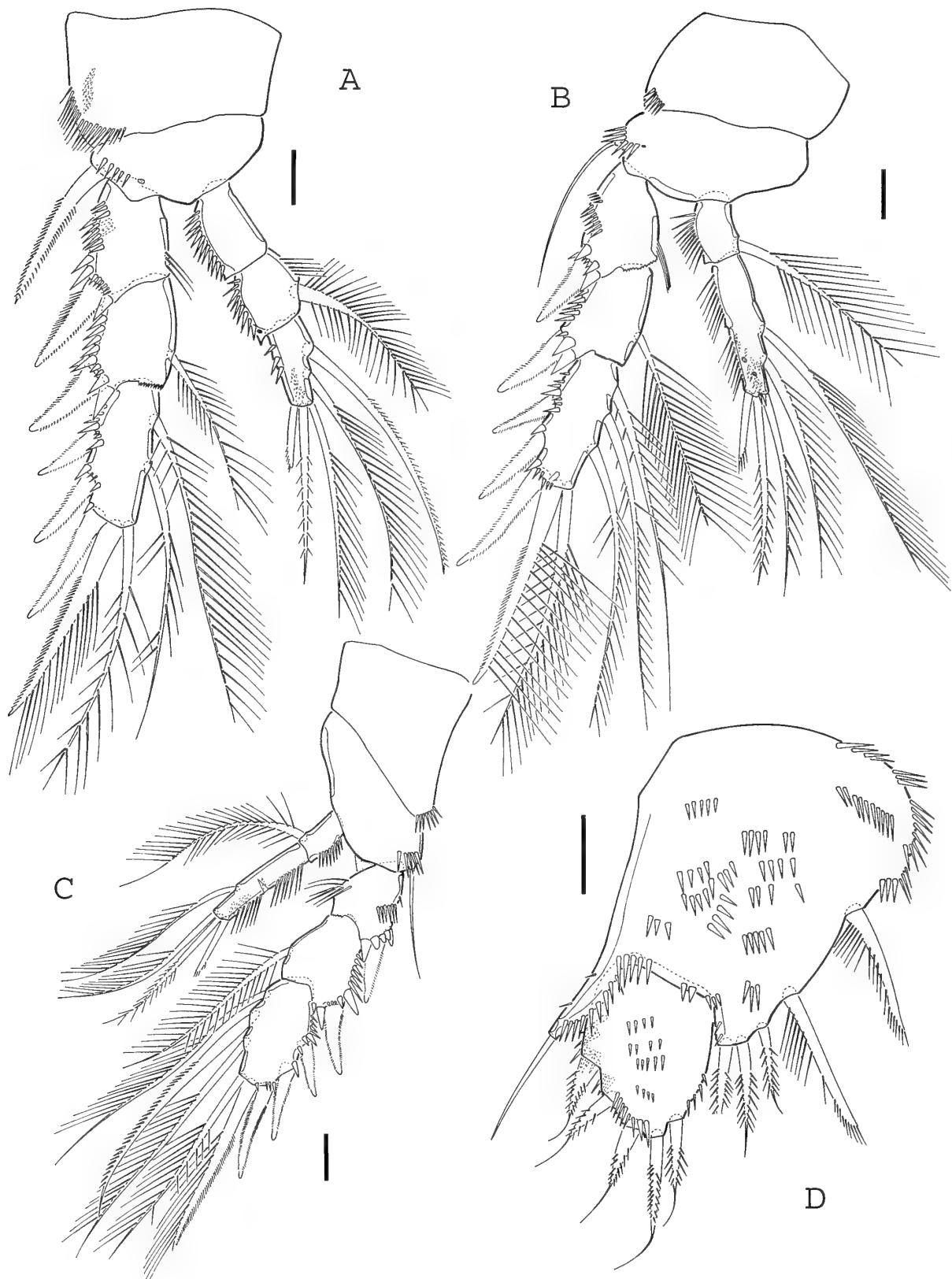


Fig. 11 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, P2; B, P3; C, P4; D, P5. Scale bars = 20 µm.

spinular rows as indicated in Fig. 10D; basis with a spinular row and seta along palmar margin, with spinules along outer distal margin; endopod represented by acutely recurved claw, spinulose along the distal inner margin, with proximal accessory seta.

P1 (Fig. 10B) Rami prehensile; coxa with spinular rows along inner and outer margins; basis with pinnate seta subdistally at outer margin and spine near articulation with endopod; spinular rows present along inner and outer margins and on anterior face. Exopod 3-segmented, 1.3 times as long as endopod (excluding apical elements); exp-1 with distal pinnate seta and spinular rows along outer margin; exp-2 elongate, 2.1 times as long as exp-1, with short, slender inner seta distally and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate, with outer spinular row; enp-2 0.3 times as long as enp-1, with outer spinular row and bearing geniculate spine, claw, and short, slender inner seta distally.

P2–P4 (Figs 11A–C) with 3-segmented exopods; endopod 3-segmented in P2 and 2-segmented in P3–P4 with the distal segment comprised of two fused segments; indentations mark the plane of fusion. Coxae with spinular rows at outer distal corner and posteriorly near outer margin of P2. Bases with outer bipinnate spine (P2) or naked seta (P3–P4), spinules, and a pore (P2–P3) near outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P2–P4 terminal endopodal segments. Spinular rows present on posterior surfaces of P4 exp-1, -2, and -3 in the paratype. Pores present as illustrated (Figs 11A–C). Seta and spine formula of P2–P4 as in Table 1.

P5 (Fig. 11D) biramous, not fused medially. Baseoendopod with numerous anterior surface and marginal spinular rows; endopodal lobe triangular, with 3 bipinnate and 2 pinnate setae; outer basal seta slender and arising from cylindrical process. Exopod 1.2 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer bipinnate spines with flagellate tips. A posterior margin row of spinules on the baseoendopod was left out of the illustration to increase clarity.

MALE. Body length (from Bergen museum paratypes) measured from anterior margin of rostrum to posterior margin of caudal rami: $\bar{x} = 506 \mu\text{m}$ ($n = 2$); without rostrum and caudal rami: $\bar{x} = 454 \mu\text{m}$ ($n = 2$). Body width: $\bar{x} = 264 \mu\text{m}$ ($n = 2$). Not all sensillae shown in habitus views (Figs 12A–B). Sexual dimorphism in body size, rostrum, antennule, P2 endopod, P5, and urosome segmentation (Figs 12A–B). The P6 could not be observed.

Rostrum (Fig. 12B) oval, twice as wide as long; with two sensillae anteriorly and one sensilla on each mediolateral margin; with mid-dorsal pore.

Antennule (Figs 12E–F) 6-segmented, chirocer; segment 5 not conspicuously swollen; segments 3 and 5 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; segment 5 with aesthetasc (55 μm long) and anterior distal corner produced into blunt apophysis; with setal formula 1–[1], 2–[1], 3–[9], 4–[9], 5–[8 + (1 + ae) + 4 modified], 6–[6 + acrothek].

P2 (Fig. 12D) as in ♀ except for endopod. Endopod 2-segmented with the distal segment derived by fusion of two segments. Enp-1 with outer row of spinules. Enp-2 with pronounced indentations marking the plane of fusion and continuous cuticle between fused segments; with spinulose outer margin; inner margin with 3 pinnate setae; distal margin with short distally pinnate spine and long bipinnate spine; posterior face with spinules. Pore present as illustrated (Fig. 12D).

P5 (Fig. 12C) baseoendopods fused medially forming transversely elongate plate (one half of plate illustrated); each side with 2 setae, slender outer basal seta arising from cylindrical process, and spinules around articulation with exopod. Exopod as in ♀ except for an additional small, bipinnate seta along the outer margin, and fewer spinular rows.

NOTES.

The holotype urosome is damaged showing a break between urosomites 3 and 4. The distal portion of the urosome is reillustrated here to provide additional information for the anal somite and caudal rami.

Inspection of the holotype and paratypes revealed that what Geddes (1968a) illustrated as discrete segments 4 and 5 of the female antennule is in reality a single segment. This segment has a surface suture, which Geddes illustrated as a functional articulation between two segments, running subdistally from the anterior towards the posterior margin. However, the surface suture is incomplete and does not reach the posterior margin. Also, the continuity of the cuticle along the posterior margin further supports the interpretation of a single compound segment rather than two distinct segments.

The male P2 endopod also has a fusion not described by Geddes (1968a). The two distal segments are fused into a single segment indicated by a continuous cuticle running through the plane of fusion. The membranous insert indicating the line of fusion (Fig. 12D) and the outer corner projection on what Geddes illustrated as the second segment may have been the source of his misinterpretation of the endopod segmentation.

This redescription has revealed additional setae, not found in Geddes' description, on the following appendages in the female: antennule (segments 2–6), antenna (allobasis and endopod), mandible (exopod and endopod), maxillule (coxal and basal endites), maxilla (syncoxal endites and endopod), maxilliped (endopodal claw), P1 and P4 (basis), and caudal rami. Additional setae were also found on the male antennule (segments 2–6).

Neozausodes limigenus (Jakobi, 1954) comb. nov.

TYPE LOCALITY. Brazil, Paraná State; Baía de Paranaguá, Ilha do Mel, Mar de Dentro.

NOTES.

Jakobi's (1954) deficient description is very brief and contains several internal inconsistencies (Lang, 1965). According to the author the male is unknown but in the description of *Z. paranaguaensis* he states that there is no sexual dimorphism in the swimming legs. He further claims that the armature formula of P2–P4 is identical in *Z. limigenus* and *Z. stammeri*, however, according to his table on p. 223 the outer spine of P4 enp-2 is missing in the former. This character, which was not figured by Jakobi, is unique within the former *Zausodes* complex and requires confirmation. The species is placed in *Neozausodes* on account of the 7-segmented ♀ antennule, the presence of large uniserrate spines on the penultimate segment of this appendage, and the round P5 exopod.

Neozausodes paranaguaensis (Jakobi, 1954) comb. nov.

TYPE LOCALITY. Brazil, Paraná State; Baía de Paranaguá, Ilha do Mel, Mar de Dentro.

NOTE.

According to Jakobi (1954) males of this species possess a small inner seta on P3–P4 exp-1. Since the author did not illustrate but only tabulated this character, and none of the other species of the

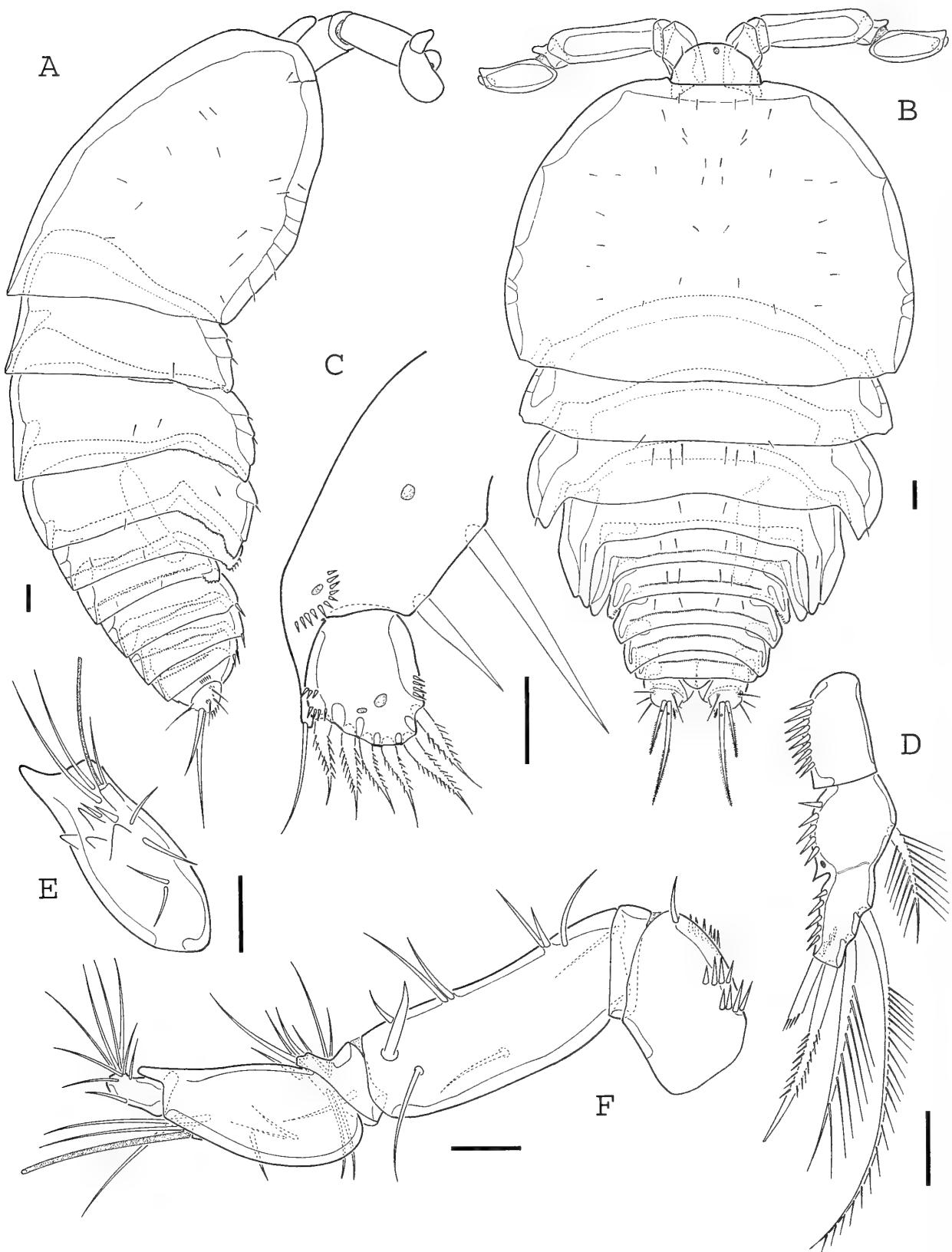


Fig. 12 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (σ°). A, Habitus, lateral view; B, habitus, dorsal view; C, P5; D, P2 endopod; E, antennule, segment 5, anterior view; F, antennule, dorsal view. Scale bars = 20 μm .

former *Zausodes* complex displays such kind of sexual dimorphism, we regard this observation as extremely doubtful. The first exopod segment of legs 2–4 often has an inner tuft or row of long setules which can easily be misinterpreted as a small seta. The species is placed in *Neozausodes* on the same grounds as for the previous one.

Neozausodes stammeri (Jakobi, 1954) comb. nov.

TYPE LOCALITY. Brazil, Paraná State; Baía de Paranaguá, Ilha do Mel, Mar de Dentro.

NOTE.

This is the most completely described of Jakobi's (1954) species. There is, however, no doubt that this species requires redescription before it can be unambiguously identified. Given the limited detail in the illustrations, the differences between *N. limigenus* and *N. stammeri* are not impressive, raising the suspicion that both are conspecific.

Neozausodes sextus (Lang, 1965) comb. nov.

TYPE LOCALITY. California, Monterey Bay, off Hopkins Marine Station; sand at about 7 m depth.

Neozausodes shulenbergeri sp. nov.

SYNONYMY. *Zausodes* cf. *arenicolus* *sensu* Ravenel & Thistle (1981) [ecology]. *Zausodes arenicolus* *sensu* Varon & Thistle (1988) [ecology].

TYPE LOCALITY. Gulf of Mexico: 29°51'N, 84°31'W (about 50 m north of day mark #2), St. George Sound, Florida, 5 m depth, unvegetated medium sand (median grain size = 0.254 mm); a seagrass meadow occurs about 150 m to the north; see Foy & Thistle (1991) for additional description.

MATERIAL EXAMINED.

The Natural History Museum: holotype ♀ in alcohol (BMNH 1999.192); allotypic paratype ♂ in alcohol (BMNH 1999.193); other paratypes are 1 ♀ in ethanol (BMNH 1999.194) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.195–198).

National Museum of Natural History (Smithsonian Institution, Washington, D.C.); additional paratypes represented by 2 ♀ ♀ and 1 ♂ in alcohol (USNM 288448–449) and 2 ♀ ♀ and 2 ♂ ♂ on slides (USNM 288447).

DESCRIPTION. All illustrations are from paratypes except Figs 13C–D which are from the holotype.

FEMALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 443 µm ($\bar{x} = 451$ µm, $n = 4$); without rostrum and caudal rami: 411 µm ($\bar{x} = 419$ µm, $n = 4$). Body (Figs 13C–D, 16A,C) dorsoventrally flattened. Greatest width: 193 µm ($\bar{x} = 196$ µm, $n = 4$) near posterior margin of cephalosome. Naupliar eye distinct; reddish brown in fresh, unstained specimens; invisible in cleared specimens. Integument with surface ornamentation/sculpturing consisting of irregular pattern of fine striations and cephalothorax pitted (not illustrated). Sensillae present dorsally and dorsolaterally on cephalothorax and body somites except penultimate one (not all shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of thoracic somites thickly chitinized laterally. Third thoracic somite and urosomites 1–5 with fine spinular rows dorsally and dorsolaterally; penultimate and antepenultimate somites with ventral spinular row (Fig. 16C); anal somite with spinular rows dorsally, ventrally, and laterally on the posterior margin (Fig. 16A,C). Lateral margins of free thoracic somites with

2 sensillae. Ventral posterolateral corners of urosomites 2–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is partially exposed in dorsal aspect; with ventral pore near posterior margin; anal operculum and pseudoperculum present. Caudal rami (Figs 13C–D, 16A,C) approximately as long as wide, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string (Figs 16A,C) extending posteriorly from each caudal ramus present in some specimens.

Rostrum (Fig. 13A) prominent, bell-shaped, defined at base; with two short sensillae anteriorly and one sensilla on each mediolateral margin; with middorsal pore.

Antennule (Figs 14A–B) 7-segmented; segments 1 and 2 longest; first segment widest with several spinular rows; segment 4 with aesthetasc (35 µm long); segment 7 with acrothek consisting of 3 elements (probably 2 setae and 1 aesthetasc, however, we were unable to distinguish which elements were setae and which was an aesthetasc); with setal formula 1-[1], 2-[10], 3-[7 + 2 unipinnate], 4-[3 + 1 unipinnate + (1 + ae)], 5-[1 + 1 unipinnate], 6-[6 + 2 pinnate], 7-[5 + acrothek].

Antenna (Fig. 13B). Coxa short and unornamented; allobasis with spinular row, abexopodal spinulose seta, and cuticular thinning marking original segmentation of basis and first endopodal segment; free endopod 1-segmented; lateral armature consisting of a pinnate spine, 1 long and 1 short seta; distal armature comprising 1 seta, 1 pinnate curved spine, and 4 geniculate spines, longest one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinular rows and hyaline surface frill as indicated in Fig. 13B; exopod 1-segmented with 1 lateral short seta and 1 distal bipinnate seta.

Labrum well developed, not medially incised.

Mandible (Fig. 14E). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod longer than exopod, with 1 bare and 1 pinnate lateral setae and 6 apical setae; exopod with 1 pinnate and 2 bare lateral setae, 1 pinnate and 2 bare distal setae, and subdistal spinular row.

Maxillule (Fig. 14D). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 4 setae and a spinular row; basal endite with 6 setae; endopod with 1 bare and 2 pinnate setae distally; exopod with 1 pinnate inner seta, 2 pinnate and 1 bare distal setae.

Maxilla (Fig. 14C). Syncoxa with spinular row along outer margin and 3 endites; praecoxal endite with 3 pinnate setae; coxal endites each with 2 bare setae and 1 pinnate seta; allobasis with claw and 3 bare setae; endopod 1-segmented with 4 bare setae.

Maxilliped (Fig. 14F). Syncoxa with a bipinnate seta and numerous spinular rows as indicated in Fig. 14F; basis with a spinular row and seta along palmar margin, with spinules along outer distal margin and on anterior face; endopod represented by acutely recurved claw with spinules along inner margin and proximal accessory seta.

P1 (Fig. 15C). Rami prehensile; coxa with spinular rows along outer margin and anterior face, with pore near inner distal corner; basis with bipinnate seta subdistally at outer margin and bipinnate spine at inner distal corner; spinular rows present along inner and outer margins, anterior face, and around articulation with endopod; with pore near outer seta. Exopod 3-segmented, 1.2 times as long as endopod (excluding apical elements); exp-1 with subdistal pinnate seta and spinular rows along outer margin; exp-2 elongate, 2.1 times

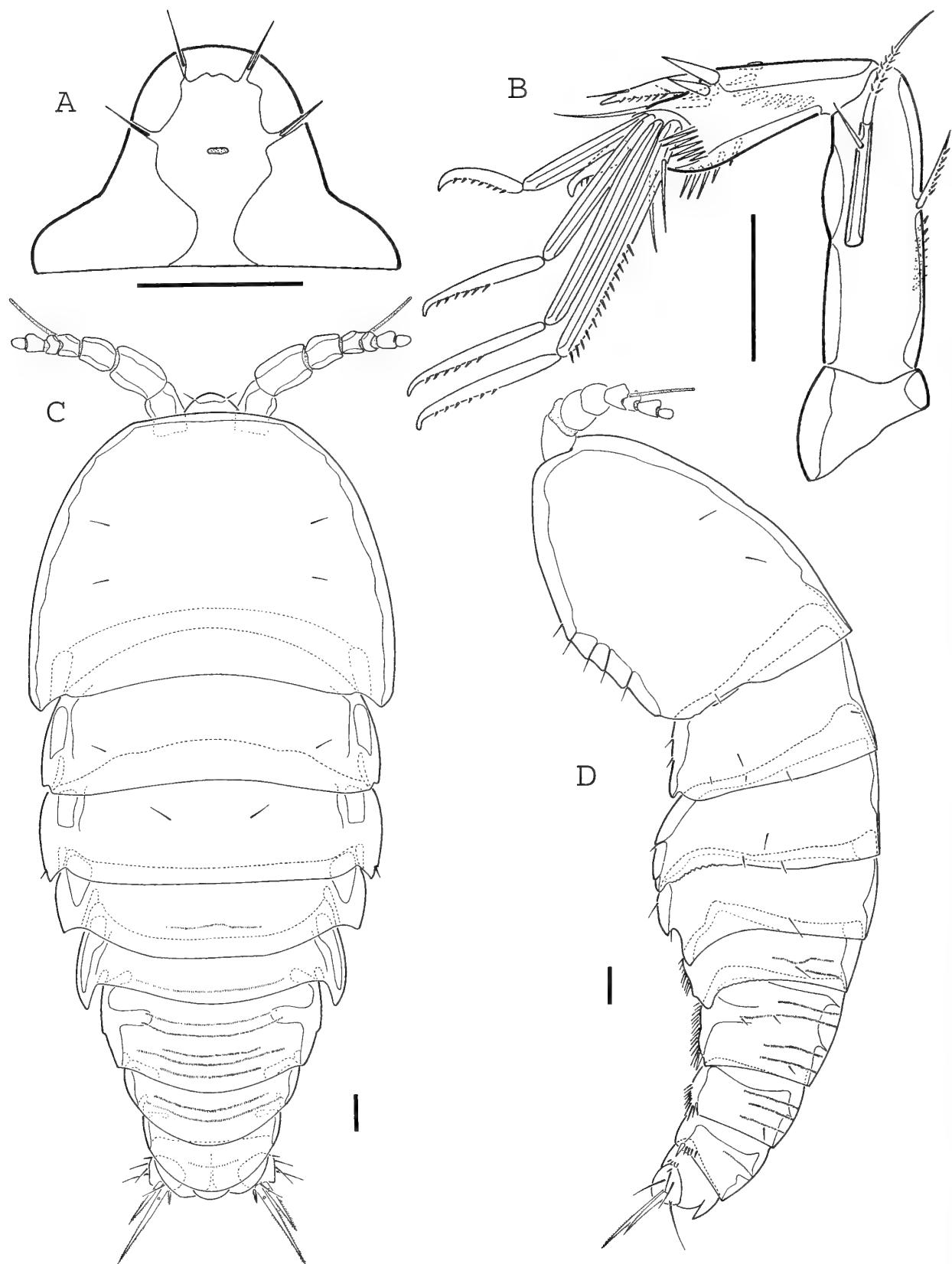


Fig. 13 *Neozausodes shulenbergeri* sp. nov. (♀). A, Rostrum; B, antenna; C, habitus, dorsal view; D, habitus, lateral view. Scale bars = 20 µm.

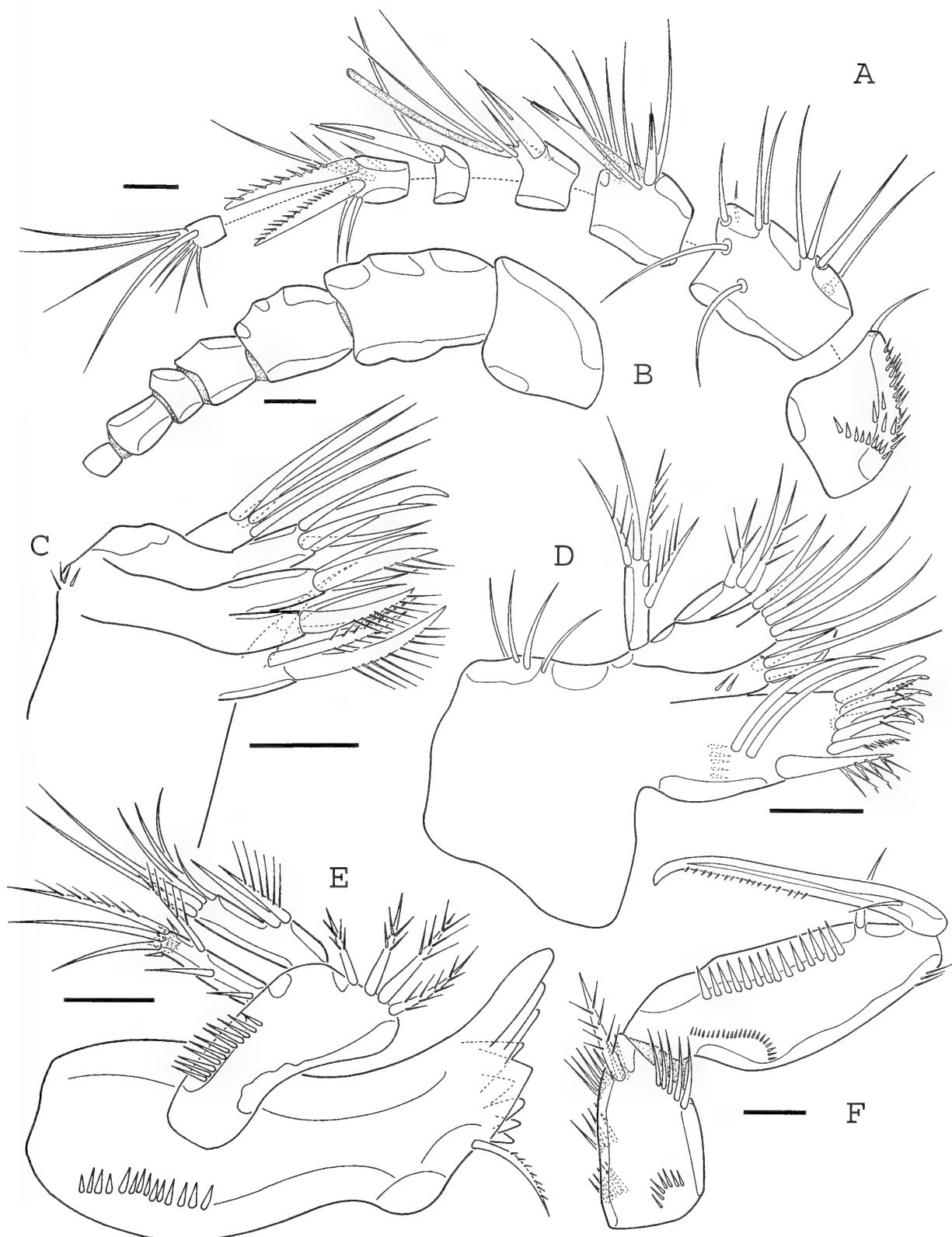


Fig. 14 *Neozausodes shulenbergeri* sp. nov. (♀). A, Antennule (disarticulated); B, antennule (armature omitted); C, maxilla; D, maxillule; E, mandible; F, maxilliped. Scale bars = 10 µm.

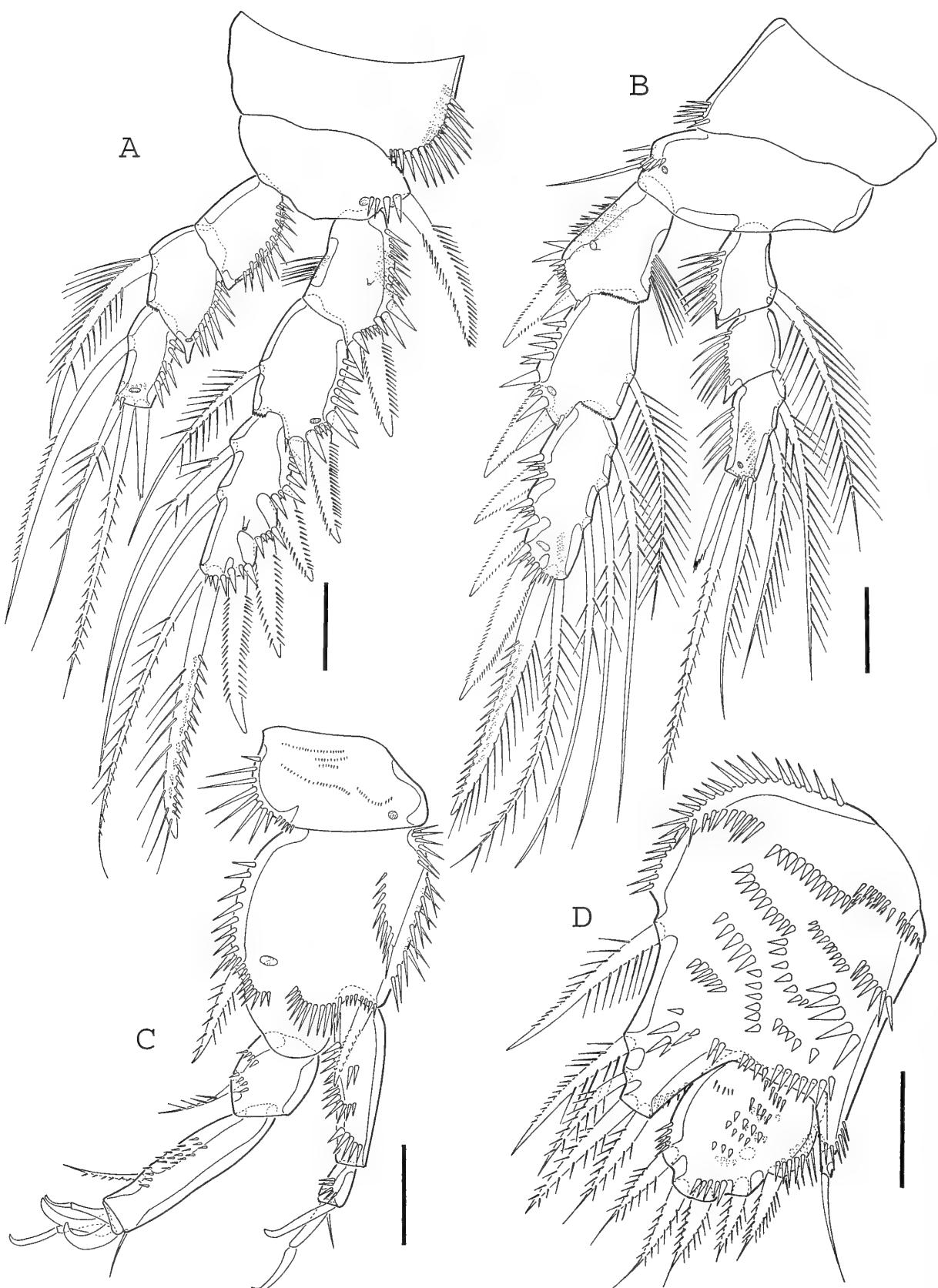


Fig. 15 *Neozausodes shulenbergeri* sp. nov. (♀). A, P2; B, P3; C, P1; D, P5. Scale bars = 20 µm.

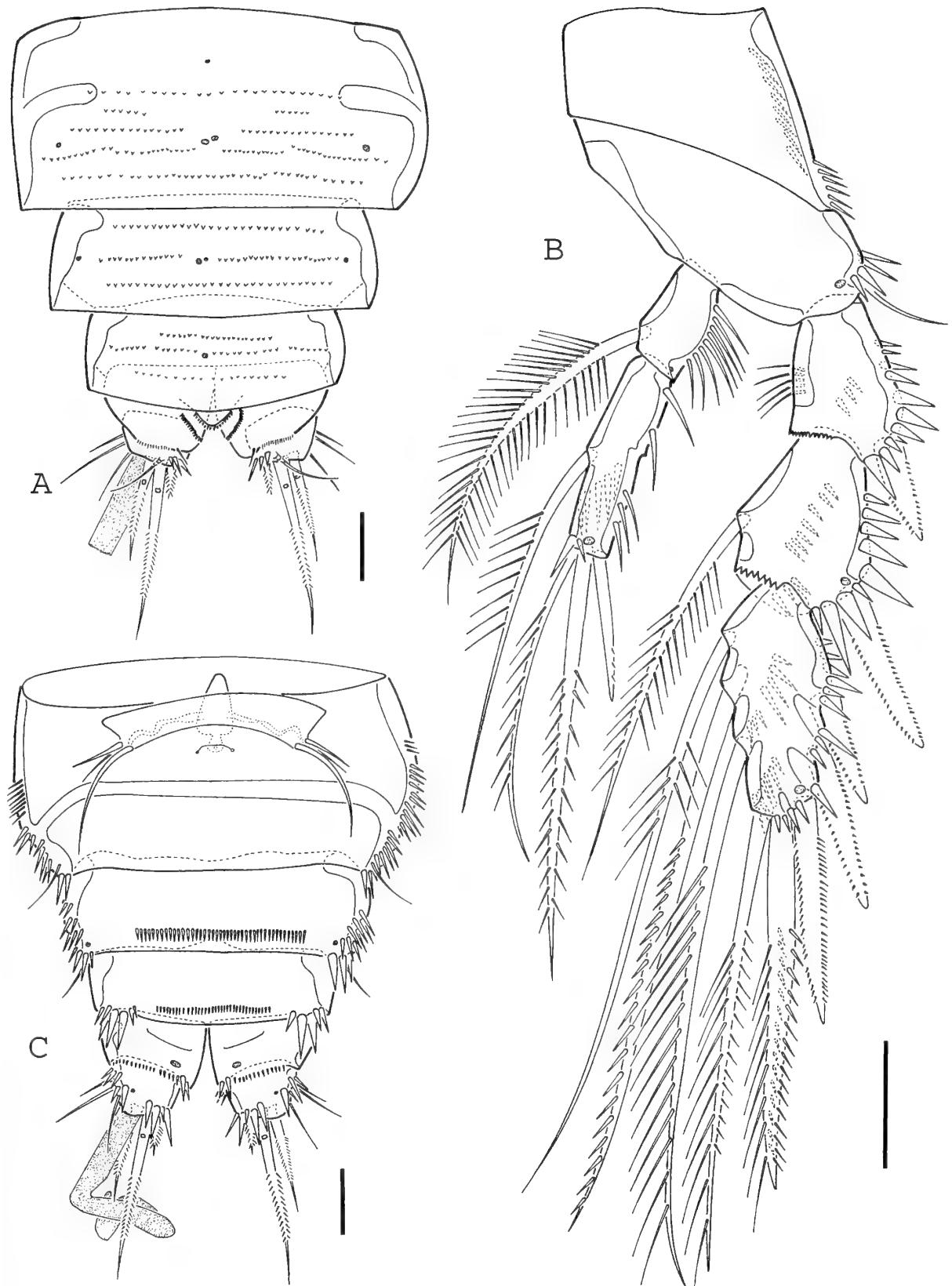


Fig. 16 *Neozausodes shulenbergeri* sp. nov. (♀). A, Urosome (excluding P5-bearing somite), dorsal view; B, P4; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20 µm.

as long as exp-1, with short, slender inner seta distally and outer margin spinular rows extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate, with outer spinular rows extending to anterior face; enp-2 0.3 times as long as enp-1, with spinular row and bearing geniculate spine, claw, and short, slender inner seta distally.

P2–P4 (Figs 15A–B, 16B) with 3-segmented exopods and endopods 3-segmented in P2 and P3 and 2-segmented in P4 with the distal segment comprised of two fused segments; indentation at outer lateral margin marks the plane of fusion. Coxae with spinular rows at outer distal corner (P2–P4) and posteriorly near outer edge of P2 and P4. Bases with outer bipinnate spine (P2) or naked seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P3–P4 exp-3, P4 exp-1 and -2, P2–P4 terminal endopodal segments. Outer distal spine of P2–P4 exp-3 tripinnate. Pores present as illustrated (Figs 15A–B, 16B). Seta and spine formula of P2–P4 as in Table 1.

P5 (Fig. 15D) biramous, not fused medially. Baseoendopod with numerous anterior surface and marginal spinular rows; endopodal lobe triangular, with 5 bipinnate setae, outermost seta with flagellate tip; outer basal seta slender and arising from cylindrical process. Exopod 1.1 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer bipinnate spines, apical, inner, and distal outer ones with flagellate tips; posterior surface with pore.

Genital double somite (Figs 16A,C) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 3 naked setae.

MALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 411 µm ($\bar{x} = 398 \mu\text{m}$, $n = 4$); without rostrum and caudal rami: 367 µm ($\bar{x} = 362 \mu\text{m}$, $n = 4$). Body width: 189 µm ($\bar{x} = 187 \mu\text{m}$, $n = 4$). Not all sensillae shown in habitus views (Figs 17A–B). Sexual dimorphism in body size, rostrum (Fig. 17D), antennule, P2 endopod and exp-3, P3 enp-3 and exp-3, P5, P6, and urosome segmentation (Figs 18B–C).

Antennule (Fig. 18A) 6-segmented, chirocerae-bearing segment not conspicuously swollen; segments 3 and 5 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; fifth segment with an aesthetasc (40 µm long), 3 modified elements, and anterior distal corner produced into blunt apophysis; with armature formula 1-[1], 2-[1], 3-[8 + 1 unipinnate], 4-[9], 5-[9 + (1 + ae) + 3 modified], 6-[5 + acrothek].

P2 (Fig. 17C) as in ♀ except for endopod and exp-3. Enp-1 with 2 outer rows of spinules. Enp-2 with outer distal corner produced into apophysis, extending one half the length of enp-3; outer margin spinulose; inner margin with subdistal bipinnate seta. Enp-3 with spinulose outer margin, short distally pinnate outer spine, long bipinnate spine distally, and 1 bipinnate inner seta; with spinules at base of distal bipinnate spine. Exp-3 without posterior spinules found in ♀. Pores present as illustrated (Fig. 17C).

P3 enp-3 and exp-3 without posterior spinules found in ♀.

P5 (Fig. 18D) biramous. Baseoendopods fused medially forming transversely elongate plate; endopodal lobe slightly developed, with 1 outer, pinnate seta and 1 inner, bipinnate seta; outer basal seta slender, arising from cylindrical process; with spinules around articulation with exopods. Exopod as in ♀ except for an additional bipinnate seta along the outer margin, fewer spinular rows, and more pores.

P6 (Fig. 18C) symmetrical; with distal seta; located more laterally than in the ♀.

ETYMOLOGY. Named for Dr. Eric Shulenberger, an administrator of scientific research who believed in the importance of taxonomy enough to fund some.

NOTES.

N. shulenbergeri sp. nov. and the three Brazilian species (Jakobi, 1954) share the presence of only 1 inner seta on P2 enp-3. Species within this group are closely related and identification is best achieved by paying particular attention to the P1 endopod and the P5 in both sexes. The sexually dimorphic spinule rows on the posterior face of P2 exp-3 and P3 exp-3 and enp-3 are unique for this species but might well have been overlooked in some other congeners.

Genus *Mucropedia* gen. nov.

DIAGNOSIS. Harpacticidae. Antennule ♀ 8-segmented, without pinnate or plumose setae on segments 1–6; without strong, modified spines on segments 3–5 or enlarged pectinate or pinnate spines on segment 6. Antennule ♂ without modified spines on segment 3. Antennary exopod 2-segmented, with armature formula [2, 2]. Maxilla with 4 spines/setae on praecoxal endite. P2–P3 endopods 3-segmented, P4 endopod 2- or 3-segmented. P2 ♀ enp-3 with 2 inner setae. P3 ♀ enp-2 without inner seta. P4 exp-3 with 2 outer spines in ♀ and 3 outer spines in ♂. P4 enp-3 (or enp-2 when 2-segmented) with 2 inner setae in both sexes. P2 ♂ enp-2 without distinct apophysis, inner seta modified into stout spine; enp-3 with 1 apical seta (inner one lost), outer spine fused to segment. P3 ♂ enp-2 outer distal corner attenuated.

Swimming leg setal formula:

	exopod	endopod
P2	0.1.223	0.1.221 [♀] 0.1.211 [♂]
P3	0.1.323	1.0.221
P4	0.1.322 [♀] 0.1.323 [♂]	1.0.221 or 1.221

P5 exopod elongate-oval in both sexes. P5 endopodal lobe ♀ not developed; distalmost inner seta rudimentary.

Sexual dimorphism in rostrum, antennule, P2 endopod, P3 endopod, P4 exopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Mucropedia cookorum* gen. et sp. nov.

OTHER SPECIES. *M. kirstenae* sp. nov.

ETYMOLOGY. The generic name is derived from the Latin *mucro*, meaning sharp point, and *pes*, meaning foot, and refers to the apophysis present on P3 enp-2 in the male. Gender: feminine.

Mucropedia cookorum sp. nov.

TYPE LOCALITY. Gulf of Mexico: 29°40.63'N, 84°22.80'W, northern Gulf of Mexico, 18 m depth, unvegetated medium sand; see Thistle *et al.* (1995) for additional description.

MATERIAL EXAMINED.

The Natural History Museum: holotype ♀ in alcohol (BMNH 1999.199); allotypic paratype ♂ in alcohol (BMNH 1999.200); other paratypes are 2 ♀ ♀ and 1 ♂ in ethanol (BMNH 1999.201–203) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.204–207).

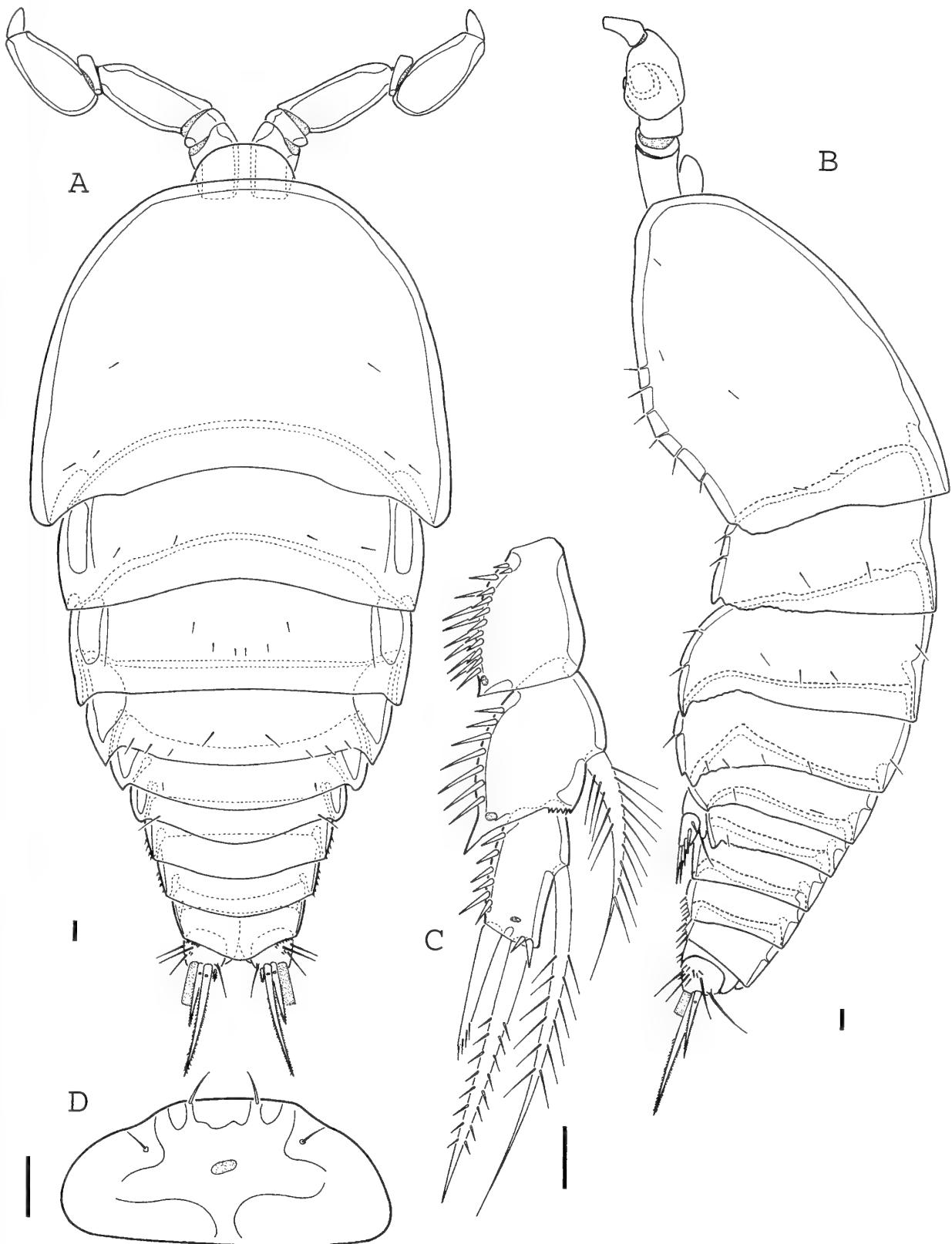


Fig. 17 *Neozausodes shulenbergeri* sp. nov. (♂). A, Habitus, dorsal view; B, habitus, lateral view; C, P2 endopod; D, rostrum. Scale bars = 10 µm.

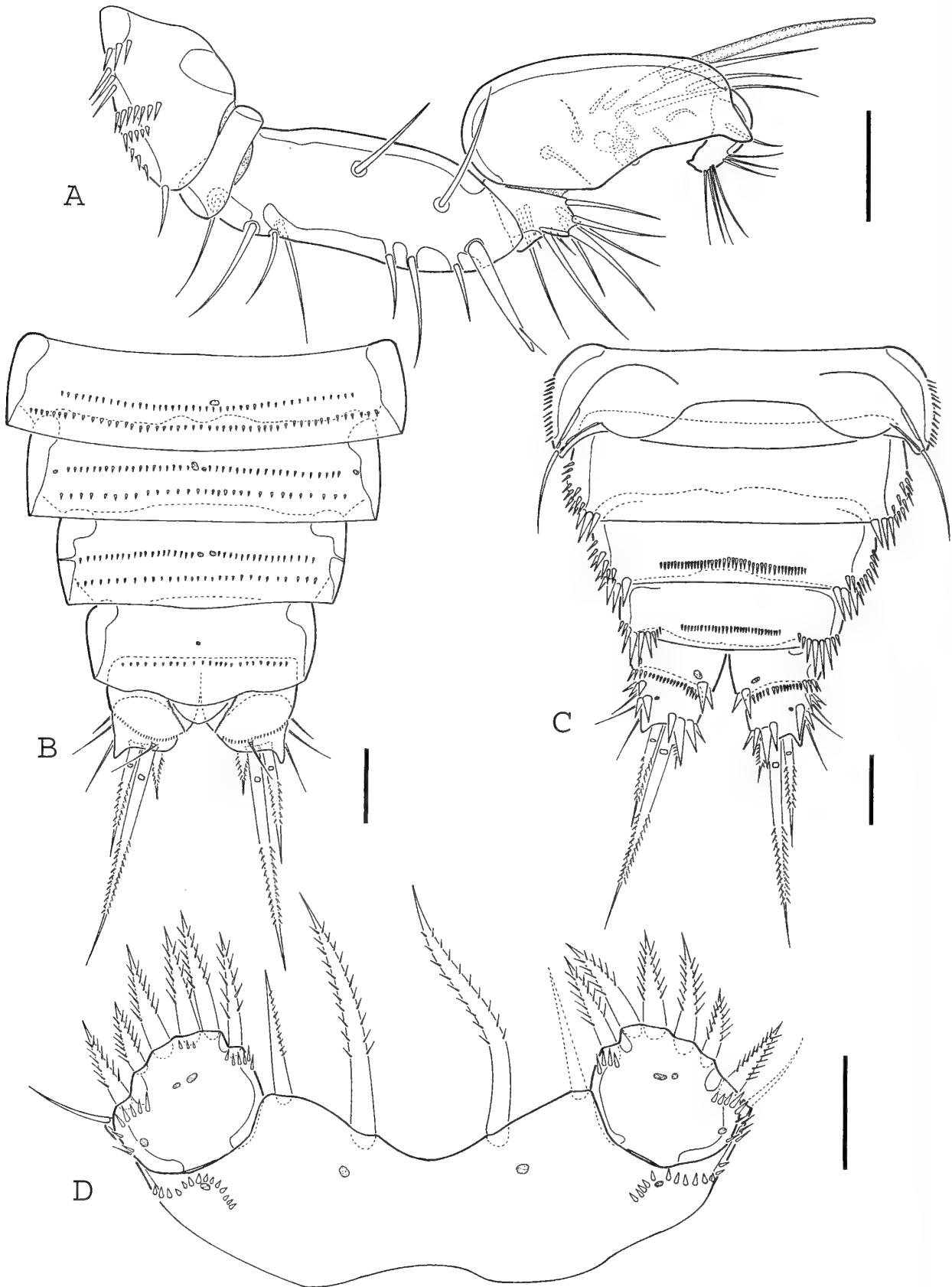


Fig. 18 *Neozausodes shulenbergeri* sp. nov. (σ). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view; D, P5. Scale bars = 20 μm .

National Museum of Natural History (Smithsonian Institution, Washington, D.C): additional paratypes represented by 3♀ and 2♂ in alcohol (USNM 288452–453) and 1♀ and 1♂ on slides (USNM 288450–451).

DESCRIPTION. All illustrations are from paratypes except 19A–B which are from the holotype.

FEMALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 288 µm ($\bar{x} = 283 \mu\text{m}$, $n = 4$); without rostrum and caudal rami: 257 µm ($\bar{x} = 246 \mu\text{m}$, $n = 4$). Body (Figs 19A–B, 20B–C) dorsoventrally flattened. Greatest width: 144 µm ($\bar{x} = 158 \mu\text{m}$, $n = 4$) near posterior margin of cephalosome. Sensillae present on cephalothorax, pedigerous somites and first, third, fourth, and sixth urosomites (not all shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of thoracic somites thickly chitinized laterally. Free thoracic somites and urosomites 1–5 with fine spinular rows dorsally and dorsolaterally; urosomite 5 with ventral spinular row; anal somite with spinular rows ventrally and laterally on the posterior margin. Lateral margins of first and second free thoracic somites with 3 sensillae; third free thoracic somite with 2 sensillae. Ventral posterolateral corners of urosomites 3–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is exposed in dorsal and ventral aspects; with two ventral pores near posterior margin; anal operculum and pronounced pseudoperulum present. Caudal rami (Figs 19A–B, 20B–C) slightly wider than long, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string extending posteriorly from each caudal ramus present in some specimens.

Rostrum (Fig. 19C) prominent, lateral margins roughly parallel to each other, defined at base; with two short sensillae anteriorly and one sensilla near each mediolateral margin; with middorsal pore.

Antennule (Fig. 20A) 8-segmented; segments 1 and 2 longest; first segment widest with spinules; fourth segment with an aesthetasc (50 µm long); apical acrothek probably consisting of 2 setae and 1 aesthetasc, however, we were unable to distinguish which elements were setae and which was an aesthetasc; with setal formula 1-[1], 2-[10], 3-[9], 4-[4 + (1 + ae)], 5-[2], 6-[4], 7-[4], 8-[4 + acrothek].

Antenna (Fig. 21A). Coxa short and unornamented; allobasis with spinular row, abexopodal seta, and surface suture marking original segment boundary between basis and first endopod segment; free endopod 1-segmented; lateral armature consisting of 1 long and 3 short setae; distal armature comprising 1 seta, 1 curved spine, and 4 geniculate spines, one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinules and hyaline surface frill as indicated in Fig. 21A; exopod 2-segmented, exp-1 with 1 lateral seta and 1 bipinnate distal seta and exp-2 with 2 distal setae.

Labrum well developed, not medially incised.

Mandible (Fig. 21B). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod with 2 lateral setae and 6 apical setae; exopod with 3 lateral setae, 3 distal setae, and spinular rows subdistally and along outer margin.

Maxillule (Fig. 21C). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 5 setae; basal endite with 6 setae; endopod with 3 distal setae; exopod with 1 inner seta and 3 distal setae.

Maxilla (Fig. 21E). Syncoxa with 3 endites; praecoxal endite with 4 setae; coxal endites each with 2 bare setae and 1 pinnate seta; allobasis with claw, 1 pinnate and 2 bare setae; endopod 1-segmented with 5 bare setae.

Maxilliped (Fig. 21D). Syncoxa with a bipinnate seta and numerous spinular rows as indicated in Fig. 21D; basis with a row of fine spinules and seta at distal palmar margin; endopod represented by acutely recurved claw with a proximal accessory seta.

P1 (Fig. 22C). Rami prehensile; coxa with spinular row along outer margin and pore at inner distal corner; basis with bipinnate seta proximal to mid-point of outer margin and spine at inner distal corner; spinular rows present along inner and outer margins, and around articulation with endopod; with pore near outer seta. Exopod 3-segmented, 1.1 times as long as endopod (excluding apical elements); exp-1 with subdistal bipinnate seta and spinular rows along outer margin; exp-2 elongate, 1.9 times as long as exp-1, with slender inner seta distally and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate with subdistal pore; enp-2 0.3 times as long as enp-1, bearing geniculate spine, claw, and short, slender inner seta distally, with distal fan of fine spinules.

P2–P4 (Figs 22A–B, 23C) with 3-segmented exopods and 3-(P2–P3) or 2-segmented (P4) endopods. Coxae with spinular rows at outer distal corner of P2 and P4. Bases with outer bipinnate spine (P2) or bare seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P3 enp-3 and P4 exp-2–3 and enp-2. Pores present as illustrated (Figs 22A–B, 23C). Seta and spine formula of P2–P4 as in Table 1.

P5 (Figs 23A–B) not fused medially. Baseoendopod with anterior surface and marginal spinular rows; with 1 short, bare and 4 long, bipinnate inner setae; outer basal seta slender and arising from cylindrical process. Exopod 1.9 times as long as wide (excluding distal spines) with numerous anterior, posterior, and marginal spinular rows; with 1 inner, 1 apical and 3 outer pinnate spines; posterior surface with pore.

Genital double-somite (Figs 20B–C) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 3 naked setae.

MALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 225 µm ($\bar{x} = 235 \mu\text{m}$, $n = 4$); without rostrum and caudal rami: 194 µm ($\bar{x} = 202 \mu\text{m}$, $n = 4$). Body width: 119 µm ($\bar{x} = 126 \mu\text{m}$, $n = 4$). Not all sensillae shown in habitus views (Figs 24A–B). Sexual dimorphism in body size, rostrum (Fig. 24C), antennule, P2 endopod, P3 enp-2, P4 exp-3, P5, P6, and urosome segmentation (Figs 25B–C).

Antennule (Fig. 25A) 6-segmented, chirocer; aesthetasc-bearing segment not conspicuously swollen; segment 3 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; segment 5 with aesthetasc (30 µm long); with armature formula 1-[1], 2-[1], 3-[9], 4-[9], 5-[8 + (1 + ae)], 6-[4 + acrothek].

P2 (Fig. 22D) as in ♀ except for endopod. Enp-1 with outer row of spinules. Enp-2 with outer distal corner extending to approximately one third the length of enp-3; outer margin spinulose; inner margin with subdistal stout pinnate seta. Enp-3 with spinulose outer margin, distal spinous apophysis, and 3 inner setae.

P3 (Fig. 22E) enp-2 with outer distal corner produced into apophysis.

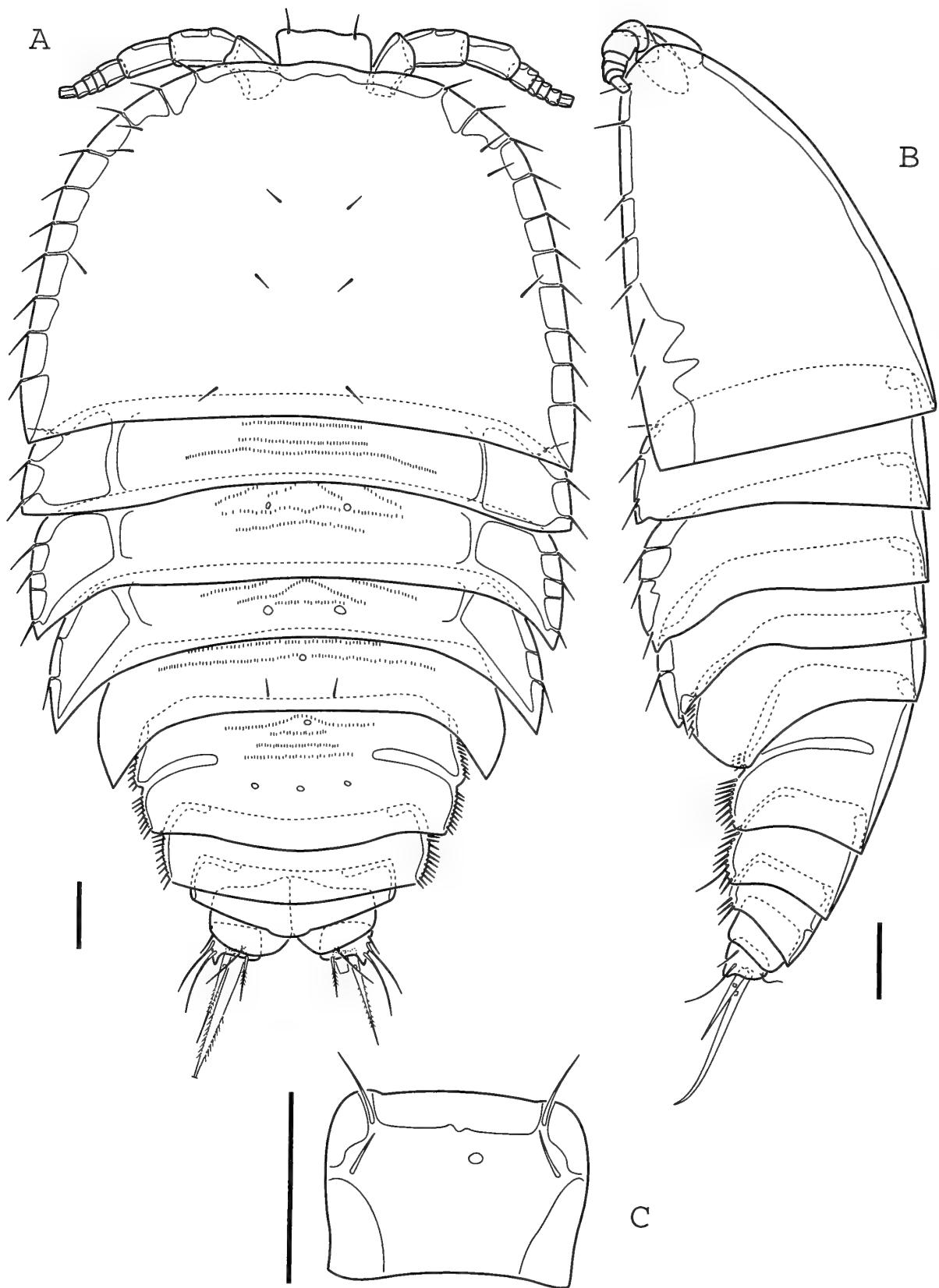


Fig. 19 *Mucropedia cookorum* sp. nov. (♀). A, habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars = 20 µm.

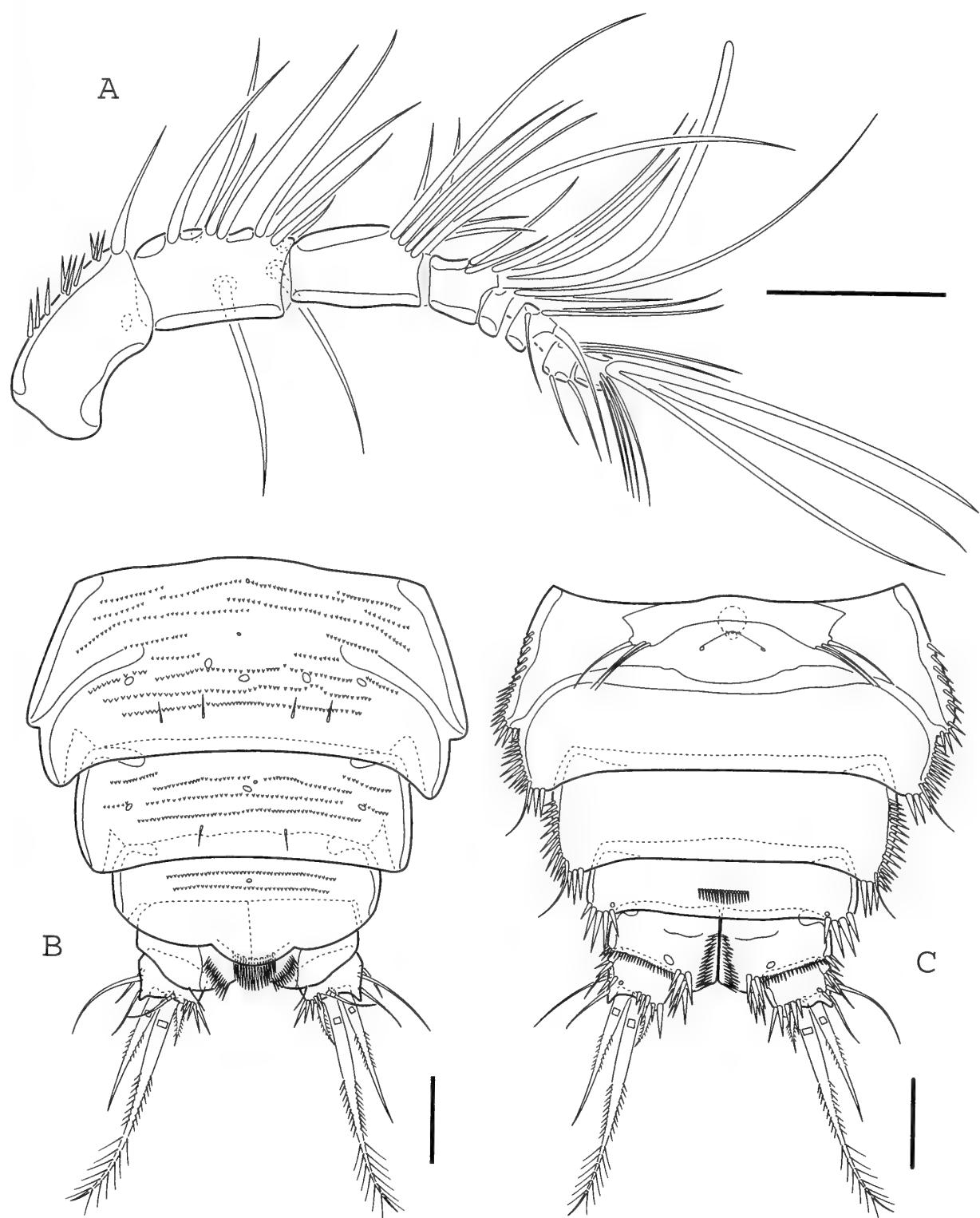


Fig. 20 *Mucropedia cookorum* sp. nov. (♀). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20 µm.

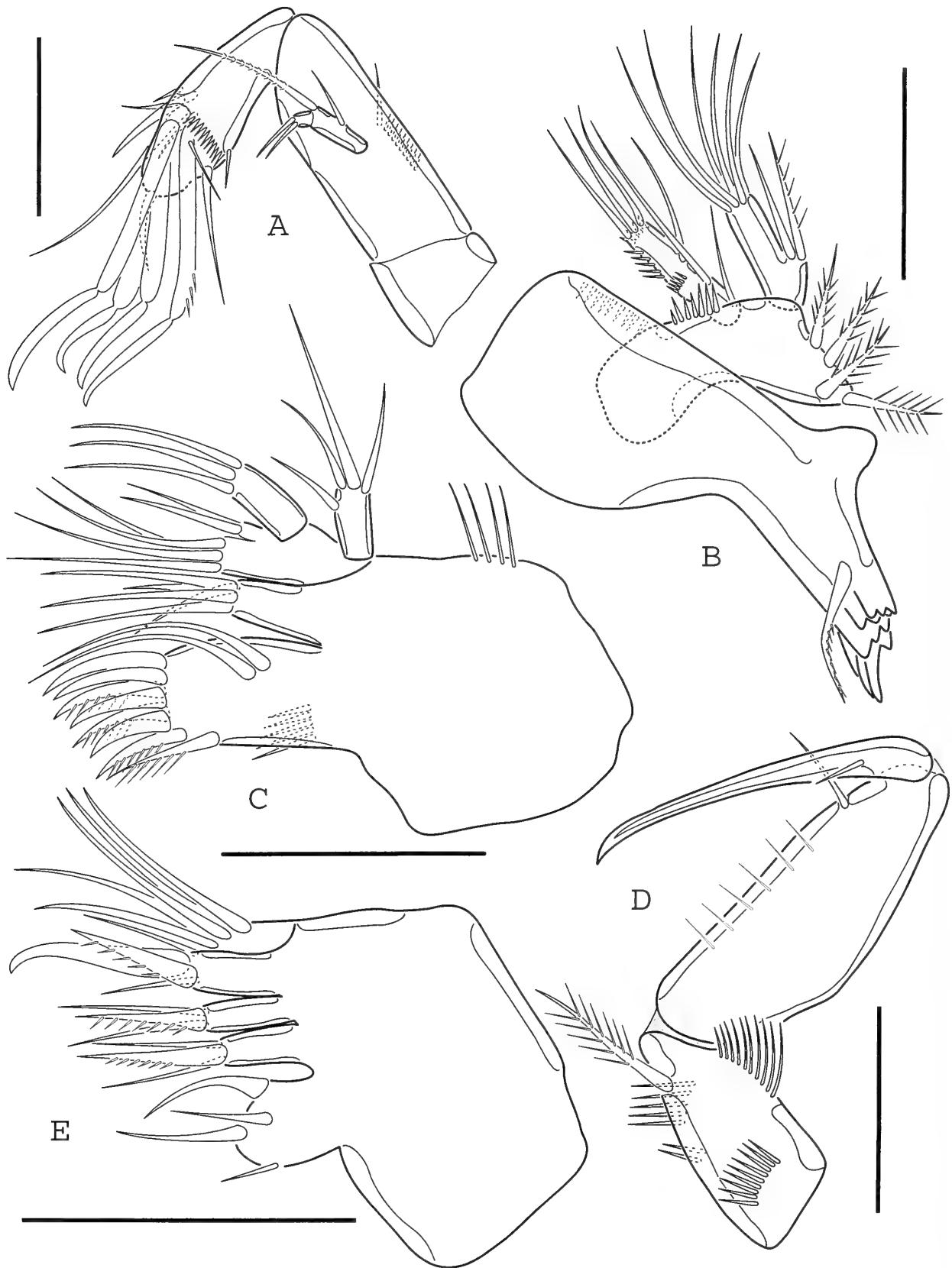


Fig. 21 *Mucropedia cookorum* sp. nov. (♀). A, Antenna; B, mandible; C, maxillule; D, maxiliped; E, maxilla. Scale bars = 20 µm.

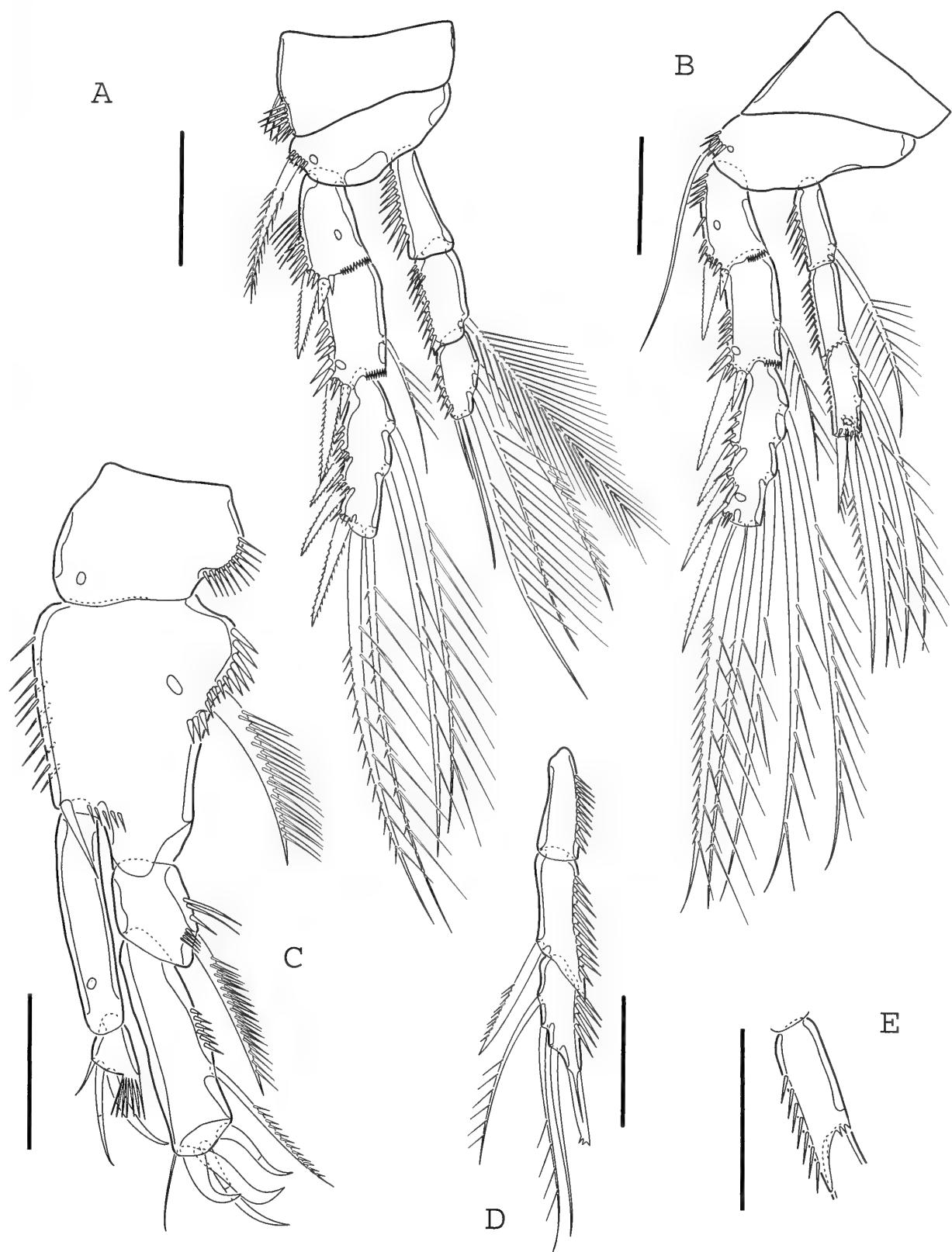


Fig. 22 *Mucropedia cookorum* sp. nov. A, ♀ P2; B, ♀ P3; C, ♀ P1; D, ♂ P2 endopod; E, ♂ P3 endopod, second segment. Scale bars = 20 μ m.

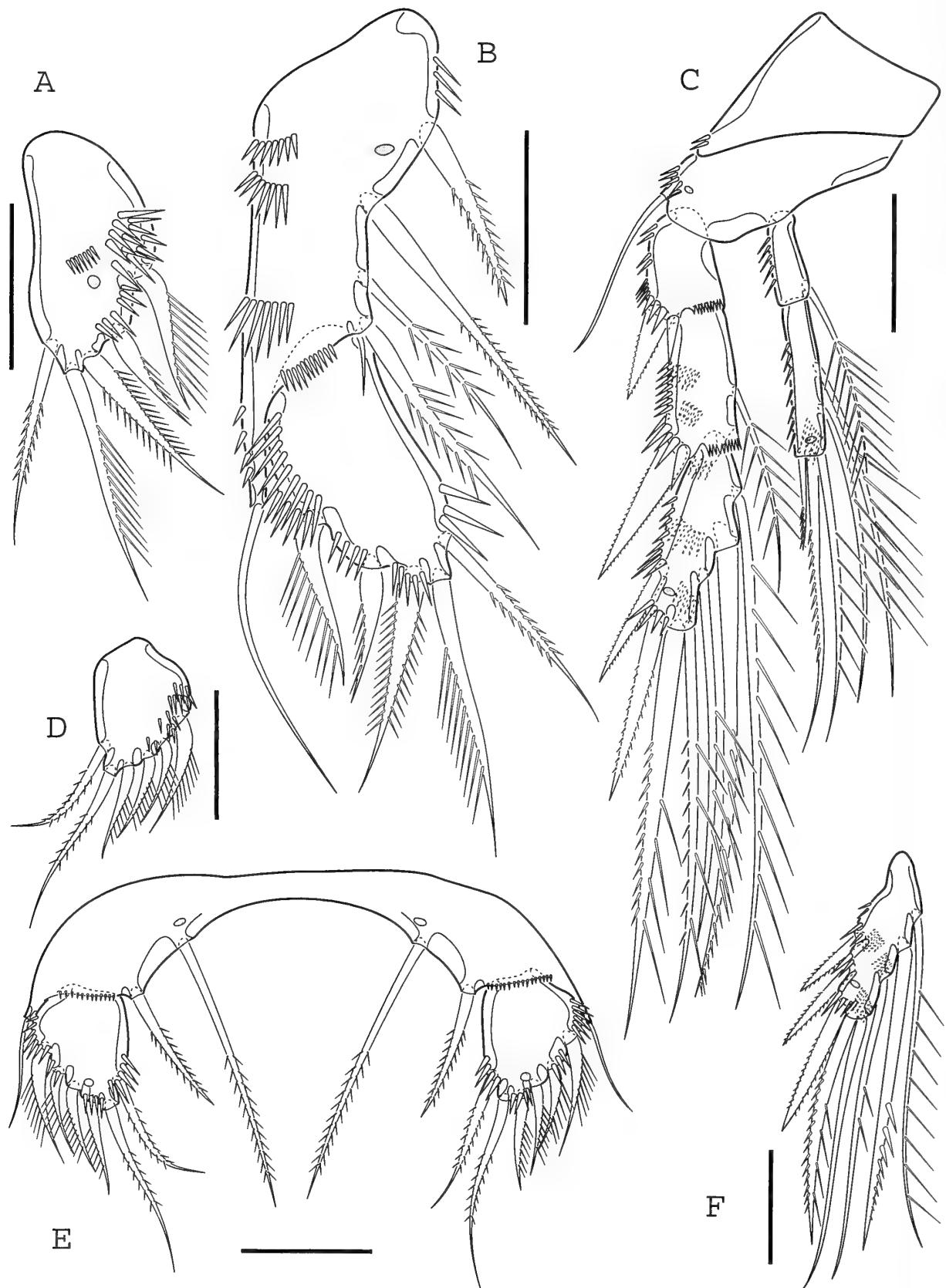


Fig. 23 *Mucropedia cookorum* sp. nov. A, ♀ P5 exopod, posterior; B, ♀ P5, anterior; C, ♀ P4; D, ♂ P5 exopod, posterior; E, ♂ P5, anterior; F, ♂ P4 exopod, third segment. Scale bars = 20 µm.

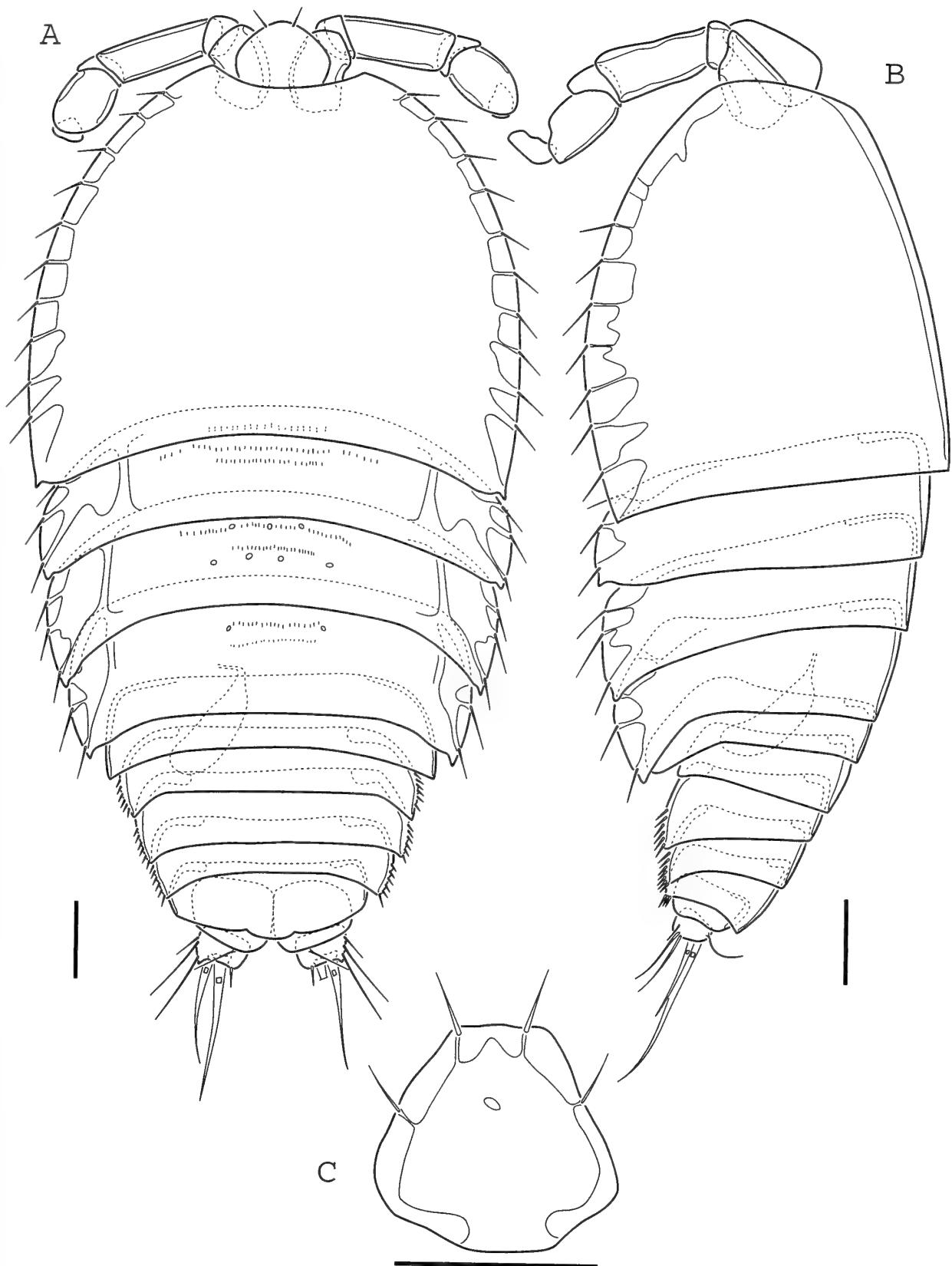


Fig. 24 *Mucropedia cookorum* sp. nov. (σ). A, Habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars = 20 μm .

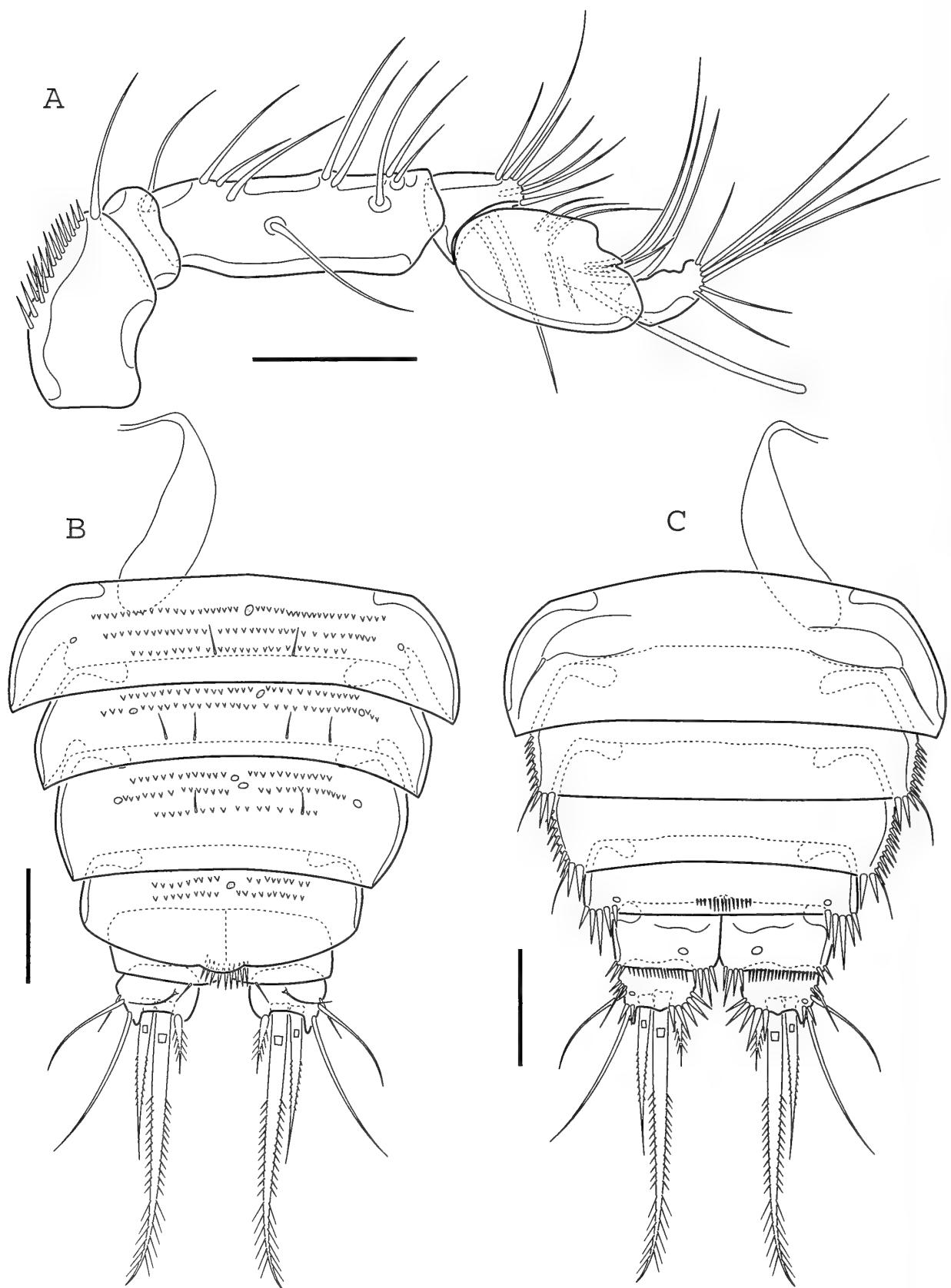


Fig. 25 *Mucropedia cookorum* sp. nov. (σ). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20 μm .

P4 (Fig. 23F) exp-3 with 3 outer bipinnate spines.

P5 (Figs 25D–E) baseoendopods fused medially forming transversely elongate plate; each side with 2 bipinnate setae, slender outer basal seta arising from cylindrical process, and spinules around articulation with exopod. Exopod 1.2 times as long as wide (excluding setae), with an additional pinnate seta along the outer margin not found in ♀, and with fewer spinular rows.

P6 (Fig. 25C) symmetrical; with distal seta; located more laterally than in ♀.

ETYMOLOGY. Named in memory of Roy Cook and in honour of Jessie Cook, the first author's grandparents.

Mucropedia kirstenae sp. nov.

TYPE LOCALITY. Gulf of Mexico: 29°40.63'N, 84°22.80'W, northern Gulf of Mexico, 18 m depth, unvegetated medium sand; see Thistle *et al.* (1995) for additional description.

MATERIAL EXAMINED.

The Natural History Museum: holotype ♀ in alcohol (BMNH 1999.208); allotypic paratype ♂ in alcohol (BMNH 1999.209); other paratypes are 1 ♀ and 1 ♂ in ethanol (BMNH 1999.210–211) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.212–215).

National Museum of Natural History (Smithsonian Institution, Washington, D.C.): additional paratypes represented by 2 ♀ ♀ and 2 ♂ ♂ in alcohol (USNM 288456–457) and 1 ♀ and 1 ♂ on slides (USNM 288454–455).

DESCRIPTION. All illustrations are from paratypes except Figs 26A–B, which are from the holotype.

FEMALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 340 µm ($\bar{x} = 320$ µm, $n = 4$); without rostrum and caudal rami: 295 µm ($\bar{x} = 276$ µm, $n = 4$). Body (Figs 26A–B, 27B–C) dorsoventrally flattened. Greatest width: 153 µm ($\bar{x} = 156$ µm, $n = 4$) near posterior margin of cephalosome. Sensillae present on cephalothorax, pedigerous somites, and third, fourth, and sixth urosomites (not all shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of pedigerous somites thickly chitinized laterally. Free thoracic somites and urosomites 1–5 with fine spinular rows dorsally and dorsolaterally; penultimate somite with ventral spinular row; anal somite with spinular rows ventrally and laterally on the posterior margin. Lateral margins of first and second pedigerous somites with 3 sensillae; third one with 2 sensillae. Ventral posterolateral corners of urosomites 3–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is exposed in dorsal and ventral aspects; with two ventral pores near posterior margin; anal operculum and pronounced pseudopericulum present. Caudal rami (Figs 26A–B, 27B–C) approximately wider than long, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string extending posteriorly from each caudal ramus not observed in specimens.

Rostrum (Fig. 26C) prominent, lateral margins roughly parallel to each other, defined at base; with two short sensillae anteriorly and one sensilla near each mediolateral margin; with middorsal pore.

Antennule (Fig. 27A) 8-segmented; segments 1 and 2 longest; first segment widest with spinules; segment 4 with aesthetasc (60 µm long); setal formula: 1-[1], 2-[10], 3-[9], 4-[4 + (1 + ae)], 5-[2], 6-[4], 7-[4], 8-[5 + acrothek]; apical acrothek consisting of 2 setae and 1 aesthetasc.

Antenna (Fig. 28A). Coxa short and unornamented; allobasis

with spinular row, abexopodal seta, and incomplete surface suture marking original segment boundary between basis and first endopod segment; free endopod 1-segmented; lateral armature consisting of 1 long and 3 short setae; distal armature comprising 1 seta, 1 spine, and 4 geniculate spines, one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with hyaline surface frill as indicated in Fig. 28A; exopod 2-segmented, exp-1 with 1 lateral seta and 1 bipinnate distal seta and exp-2 with 2 distal setae.

Labrum well developed, not medially incised.

Mandible (Fig. 28B). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod with 2 lateral setae and 6 apical setae; exopod with 3 lateral setae, 3 distal setae, and spinular rows subdistally and along outer margin.

Maxillule (Fig. 28C). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 5 setae; basal endite with 6 setae; endopod with 3 distal setae; exopod with 1 inner seta and 3 distal setae.

Maxilla (Fig. 28E). Syncoxa with 3 endites; praecoxal endite with 1 pinnate and 3 bare setae; proximal coxal endite with 1 bare seta and 2 pinnate setae; distal coxal endite with 2 bare setae and 1 pinnate seta; allobasis with claw, 1 pinnate and 2 bare setae; endopod 1-segmented with 5 bare setae.

Maxilliped (Fig. 28D). Syncoxa with a bipinnate seta and numerous spinular rows as indicated in Fig. 28D; basis with a row of fine spinules and seta along palmar margin; endopod represented by acutely recurved claw with a proximal accessory seta.

P1 (Fig. 29E). Rami prehensile; coxa with spinular row along outer margin and pore at inner distal corner; basis with bipinnate seta near mid-point of outer margin and spine at inner distal corner; spinular rows present along inner and outer margins, and around articulation with endopod; with pore near outer seta. Exopod 3-segmented, 0.9 times as long as endopod (excluding apical elements); exp-1 with subdistal bipinnate seta and spinular rows along outer margin; exp-2 elongate, 2.3 times as long as exp-1, with slender inner seta distally and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate with subdistal pore; enp-2 0.3 times as long as enp-1, bearing geniculate spine, claw, and short, slender inner seta distally, with distal fan of fine spinules.

P2–P4 (Figs 29B–C, 30A) with 3-segmented rami. Coxae with spinular rows at outer distal corner of P2 and P4 and pore at inner distal corner of P3 and P4. Bases with outer bipinnate spine (P2) or bare seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P2 enp-3, P3 enp-3 and P4 exp-2–3 and enp-3. Pores present as illustrated (Figs 29B–C, 30A). Seta and spine formula of P2–P4 as in Table 1.

P5 (Figs 30B–C) not fused medially. Baseoendopod with anterior surface and marginal spinular rows; with 4 long, bipinnate and 1 short, bare inner setae; outer basal seta slender and arising from cylindrical process. Exopod 1.9 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer pinnate spines; posterior surface with pore.

Genital double somite (Figs 27B–C) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 3 naked setae.

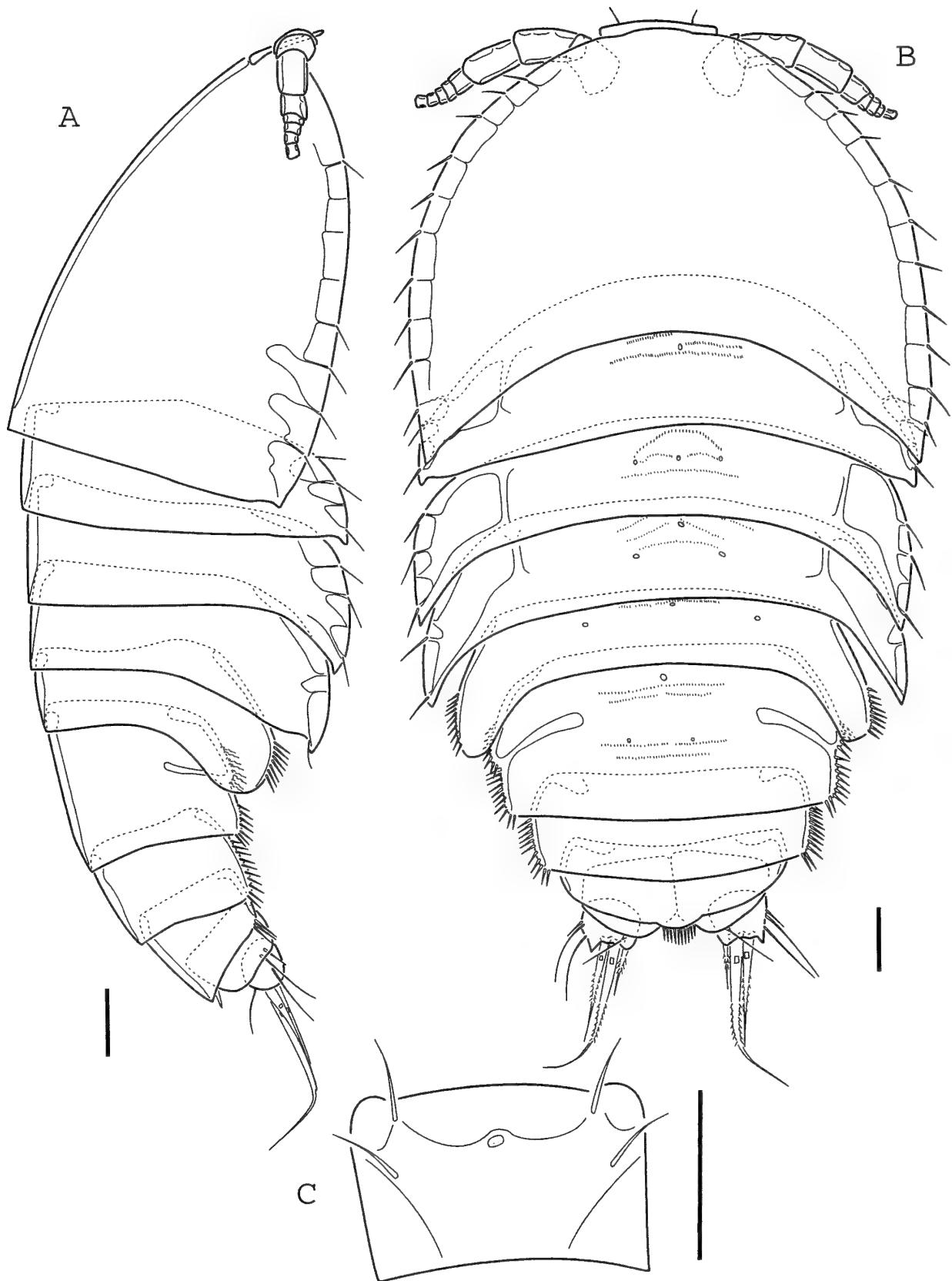


Fig. 26 *Mucropedia kirstenae* sp. nov. (♀). A, Habitus, lateral view; B, habitus, dorsal view; C, rostrum. Scale bars = 20 µm.

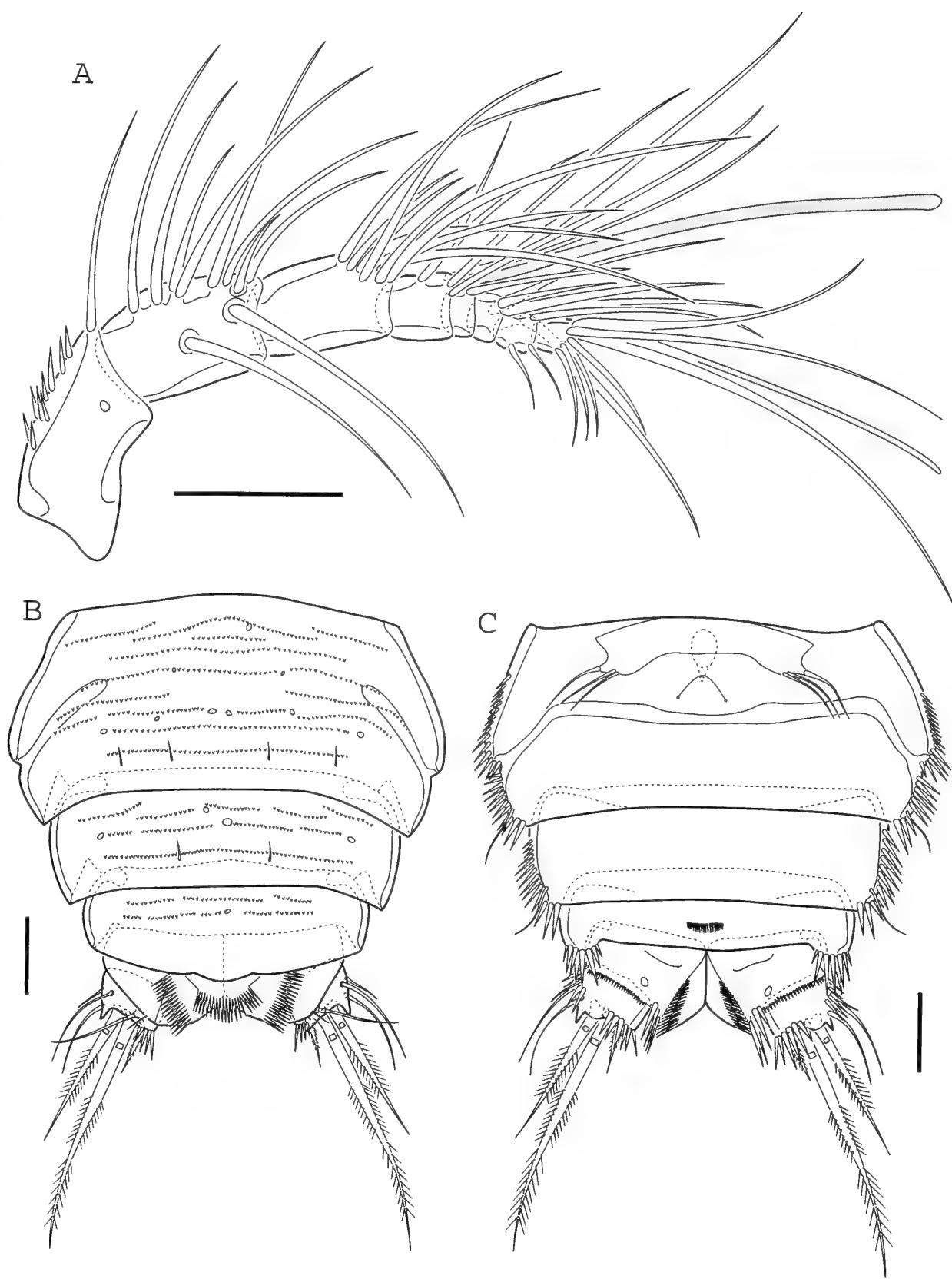


Fig. 27 *Mucopedia kirstenae* sp. nov. (♀). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20 µm.

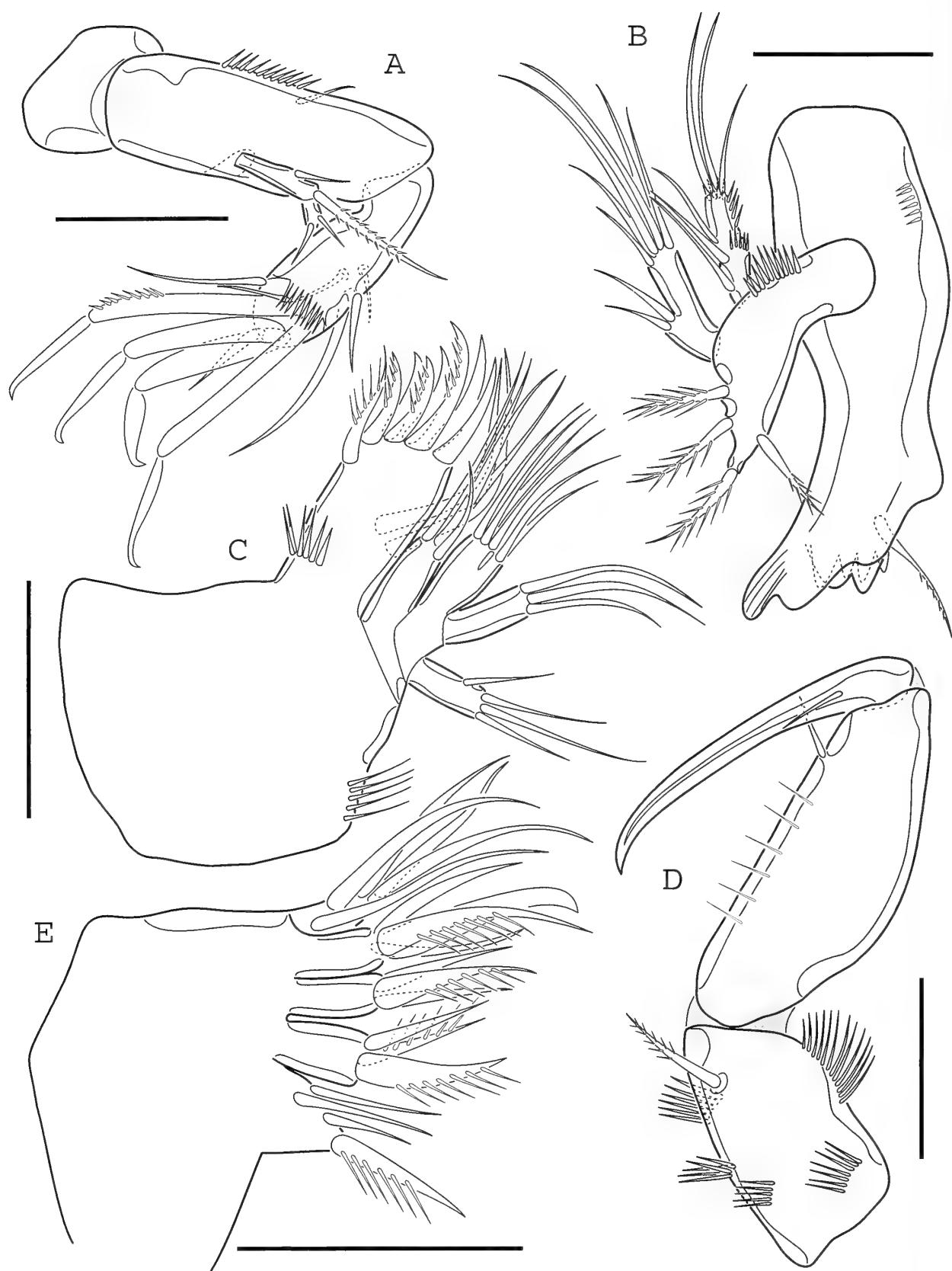


Fig. 28 *Mucropedia kirstenae* sp. nov. (♀). A, Antenna; B, mandible; C, maxillule; D, maxilliped; E, maxilla. Scale bars = 20 µm.

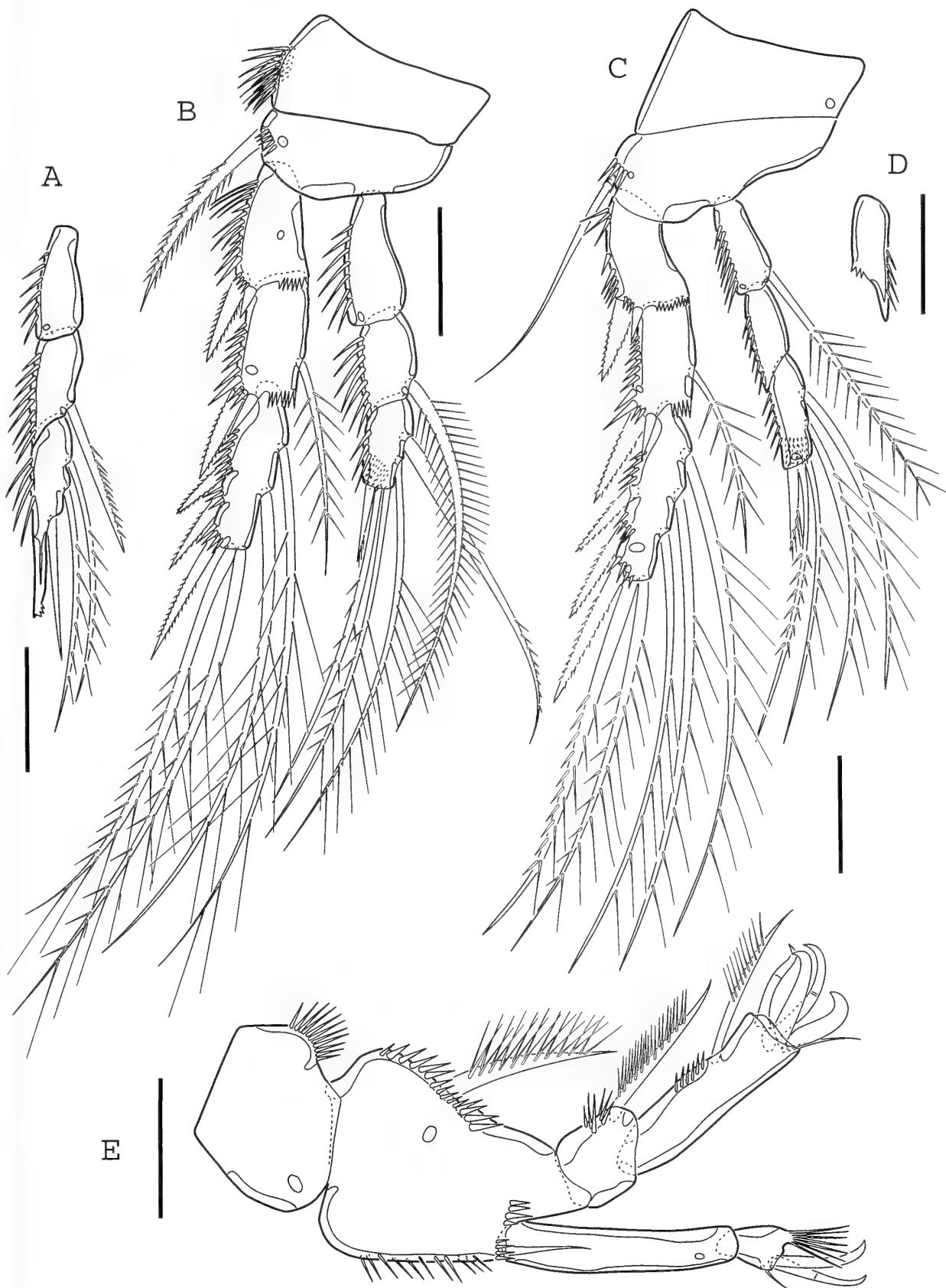


Fig. 29 *Mucropedia kirstenae* sp. nov. A, ♂P2 endopod; B, ♀ P2; C, ♀ P3; D, ♂P3 endopod, second segment; E, P1. Scale bars = 20 µm.

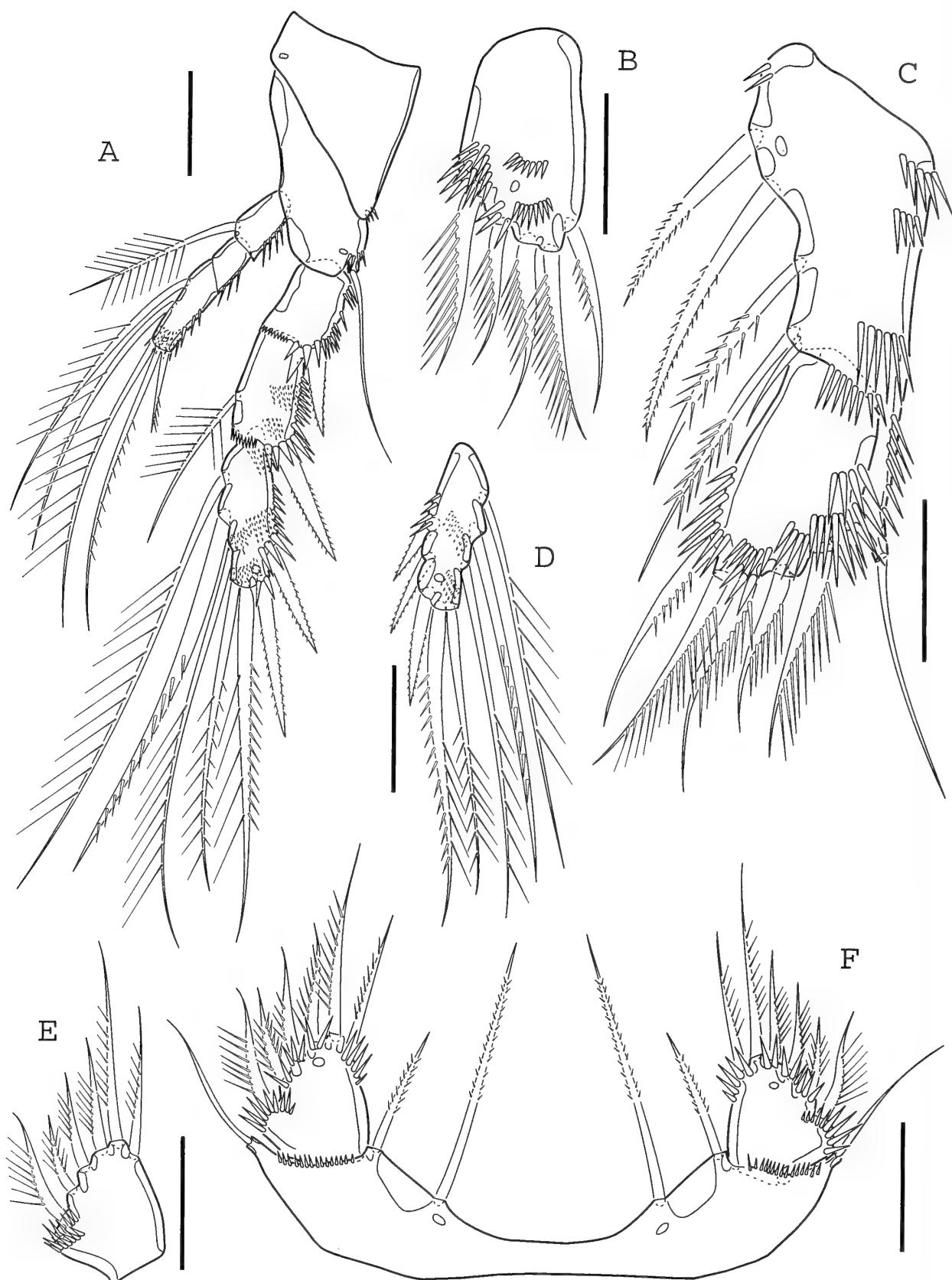


Fig. 30 *Mucropedia kirstenae* sp. nov. A, ♀ P4; B, ♀ P5 exopod, posterior view; C, ♀ P5, anterior view; D, ♂ P4 exopod, third segment; E, ♂ P5 exopod, posterior view; F, ♂ P5, anterior view. Scale bars = 20 µm.

MALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 253 µm ($\bar{x} = 249$ µm, $n = 4$); without rostrum and caudal rami: 220 µm ($\bar{x} = 217$ µm, $n = 4$). Body width: 131 µm ($\bar{x} = 134$ µm, $n = 4$). Not all sensillae shown in habitus views (Figs 31A–B). Sexual dimorphism in body size, rostrum (Fig. 31C), antennule, P2 endopod, P3 endopod, P4 exp-3, P5, P6, and urosome segmentation (Figs 32B–C).

Antennule (Fig. 32A) 6-segmented, chirocer; aesthetasc-bearing segment not conspicuously swollen; segment 3 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; segment 5 with aesthetasc (50 µm long); with armature formula 1-[1], 2-[1], 3-[9], 4-[9], 5-[8 + (1 + ae)], 6-[7].

P2 (Fig. 29A) as in ♀ except for endopod. Enp-1 with outer row of spinules and anterior pore. Enp-2 with outer distal corner extending approximately one third the length of enp-3; outer margin spinulose; inner margin with subdistal thick pinnate seta. Enp-3 with spinulose outer margin, distal spinous apophysis, and 3 inner setae.

P3 (Fig. 29D) enp-2 with outer distal corner produced into apophysis; enp-3 without pore and posterior spinules found in ♀.

P4 (Fig. 30D) exp-3 with 3 outer bipinnate spines.

P5 (Figs 30E–F) baseoendopods fused medially forming transversely elongate plate; each side with 2 bipinnate setae, slender outer basal seta arising from cylindrical process, and spinules around articulation with exopod. Exopod 1.1 times as long as wide (excluding setae), with an additional pinnate seta along the outer margin not found in ♀, and with fewer spinular rows.

P6 (Fig. 32C) symmetrical; with distal seta; located more laterally than in ♀.

ETYMOLOGY. Named for Kirsten Lambshead.

NOTES.

M. kirstenae can be readily distinguished from *M. cookorum* by the segmentation of the P4 endopod (3-segmented in *M. kirstenae*, 2-segmented in *M. cookorum*). Both species are extremely close otherwise and additional differences should be sought at the level of setal lengths and segmental proportions. It is the consistent nature of these differences rather than their magnitude that convinced us of the distinctiveness and co-occurrence of two species. The existence of sibling species is a well known phenomenon in the family Harpacticidae and makes accurate identification onerous. Soyer *et al.* (1987) demonstrated the presence of sibling species of the genus *Tigriopus* on the Kerguelen and Crozet Islands. Huys *et al.* (1996) recently pointed out that *Harpacticus obscurus* T. Scott, *H. giesbrechti* Klie and *H. littoralis* Sars are extremely difficult to separate and identification is often based on setal lengths and ornamentation, pore patterns and position of spinule rows.

Genus *Archizausodes* gen. nov.

DIAGNOSIS. Harpacticidae. Antennule ♀ 8-segmented, without pinnate or plumose setae on segments 1–6; without strong, modified spines on segments 3–5 or enlarged pectinate or pinnate spines on segment 6. Antennule ♂ without modified spines on segment 3. Antennary exopod 2-segmented, with armature formula [2, 2]. Maxilla with 4 spines/setae on praecoxal endite. P2–P3 endopods 3-segmented, P4 endopod 2-segmented. P2 ♀ enp-3 with 2 inner setae. P3 ♀ enp-2 with inner seta. P4 exp-3 with 3 outer spines in both sexes. P4 enp-2 with 2 inner setae in both sexes. P2 ♂ enp-2 without distinct apophysis, inner seta not modified; enp-3 with 1 apical seta (inner one lost), outer spine fused to segment. P3 ♂ enp-2 outer distal corner not attenuated.

Swimming leg setal formula:

	exopod	endopod
P2	0.1.223	0.1.221 [♀] 0.1.211 [♂]
P3	0.1.323	1.1.221
P4	0.1.323	1.221

P5 exopod elongate-oval in both sexes. P5 endopodal lobe ♀ not developed; distal 3 inner setae rudimentary.

Sexual dimorphism in rostrum, antennule, P2 endopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Zausodes biarticulatus* Itô, 1979 = *Archizausodes biarticulatus* (Itô, 1979) comb. nov.

OTHER SPECIES. None.

ETYMOLOGY. The generic name is derived from the Greek prefix *archi-*, meaning first, and alludes to the primitive position of the genus. Gender: masculine.

Archizausodes biarticulatus (Itô, 1979) comb. nov.

TYPE LOCALITY. Chichi-jima Island, Bonin Islands; shallow water off Miyano-hama; coarse sand with broken shells and corals.

NOTES.

Additional autapomorphies for this genus include the elongate proximal exopod segment of P1, the transversely prolonged basis of P4, and the reduction of particular setae on the exopod and baseoendopod of ♀ P5. *A. biarticulatus* shows some similarities with *Z. cinctus* (see below).

PHYLOGENY

Selection of outgroup

Lang (1944, 1948) divided the Harpacticidae in two subfamilies, Harpacticellinae and Zausodiinae, the names of which were later corrected by Vervoort (1964) as Harpacticinae and Zausodinae, respectively. The Zausodinae was proposed to accommodate *Zaus*, *Zausodes* and *Zausopsis*, all of which have a strongly dorsoventrally depressed, more or less shield-shaped body with completely developed pleurotergites on the pedigerous somites. The Harpacticinae included *Harpacticus*, *Tigriopus*, *Harpacticella* and *Perissocope* which according to Lang (1944, 1948) have a body which is 'normal, elongate and not shield-shaped'. Two more genera, *Discoharpacticus* Noodt and *Paratigriopus* Itô have been added to the latter subfamily since (Noodt, 1954; Itô, 1969).

Lang (1948: 355) remarked that *Zausodes* showed a certain resemblance with *Perissocope* in the reduced swimming leg armature but nevertheless assigned more weight to the body form, favouring a relationship with *Zaus* and *Zausopsis*. Since *Zausodes* has a short P1 exp-1, a well developed maxilliped and 2 setae on the ♂ P5 baseoendopod he was of the opinion that the genus had diverged early in the evolution of the Zausodinae. On the other hand he expressed some doubts as to the relationships of *Perissocope* since males were as yet unknown.

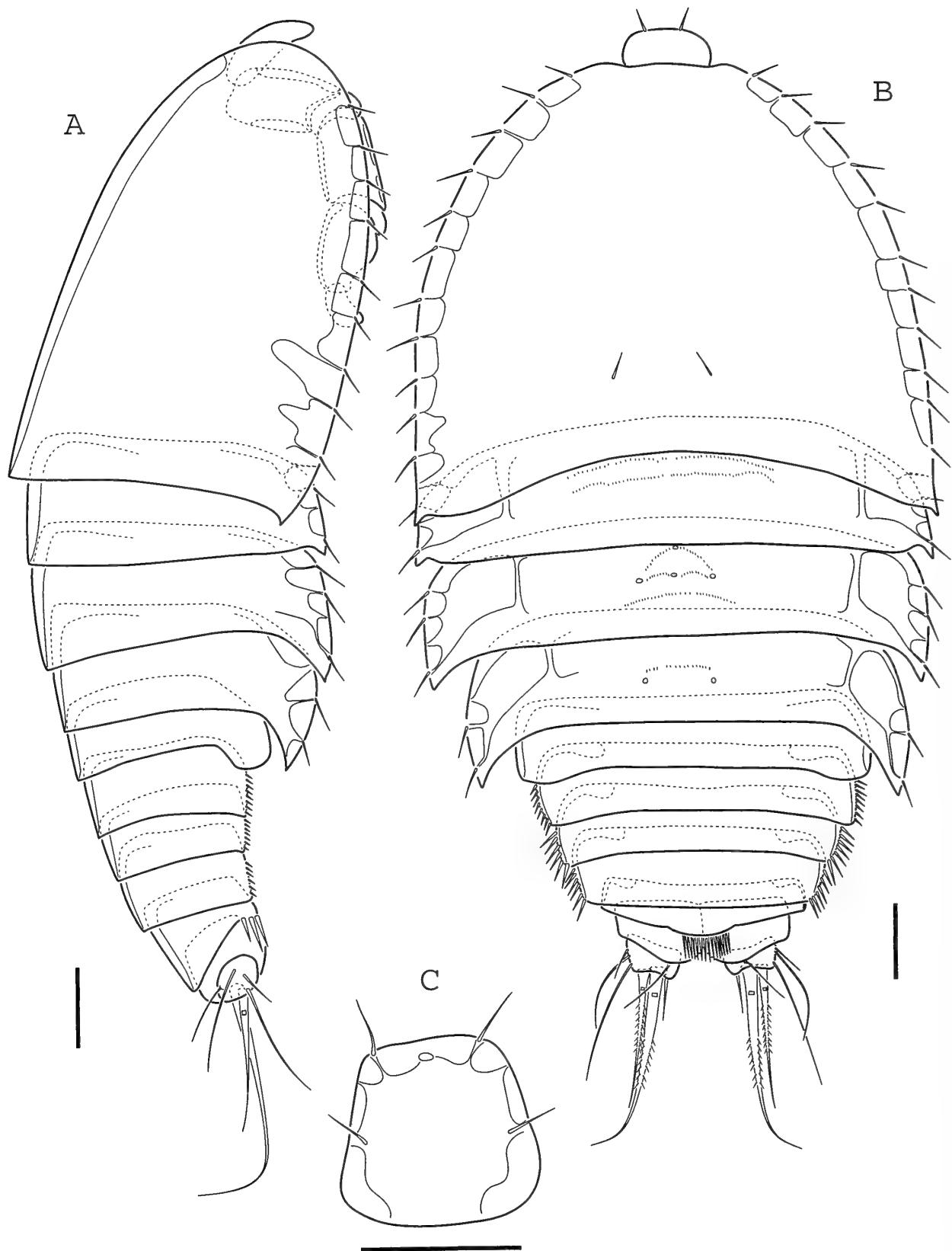


Fig. 31 *Mucropedia kirstenae* sp. nov. (♂). A, Habitus, lateral view; B, habitus, dorsal view; C, rostrum. Scale bars = 20 µm.

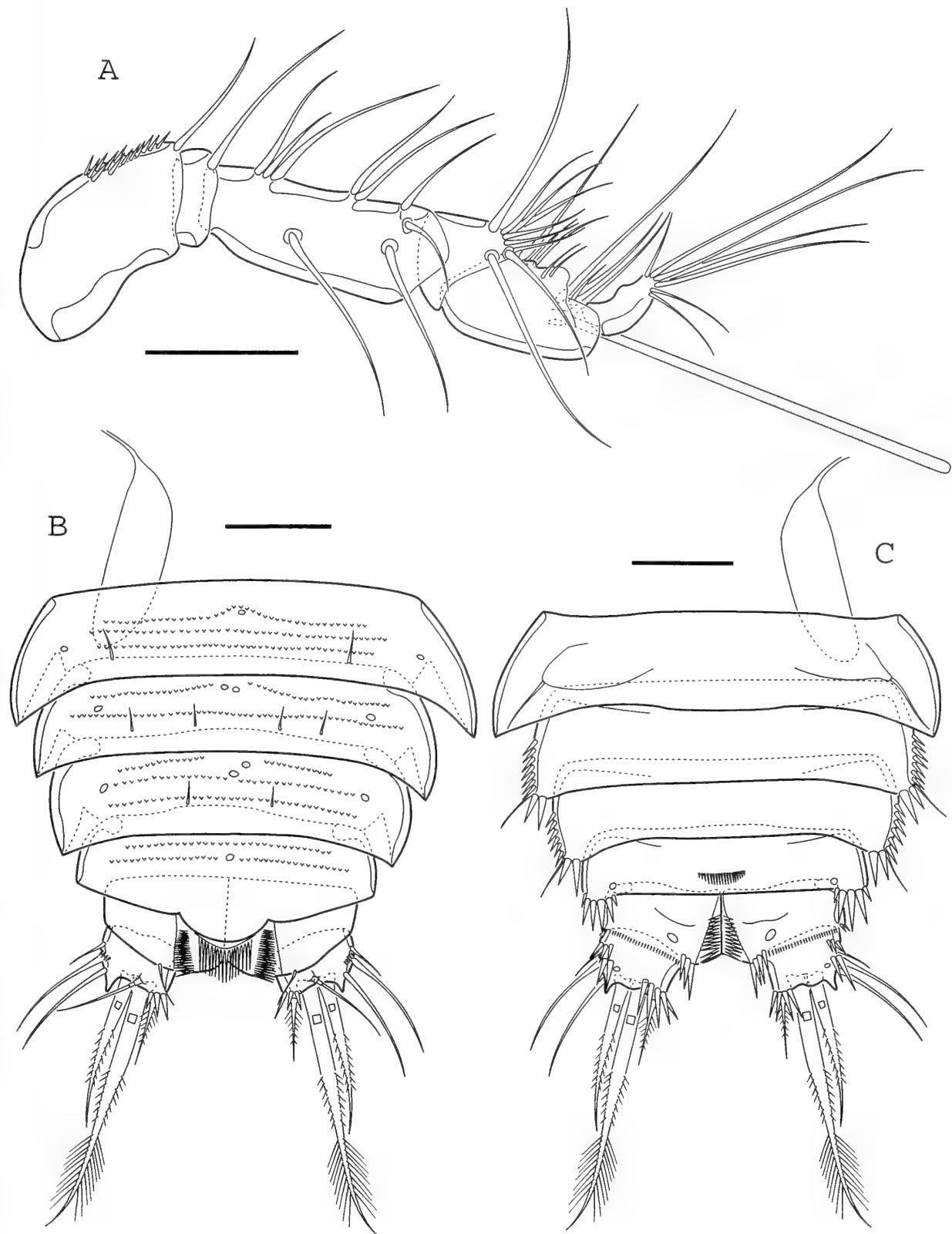


Fig. 32 *Mucropedia kirstenae* sp. nov. (♂). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20 µm.

A first indication of the artificiality of Lang's subdivision was given by Itô (1979) who noted the similarity between the shape of the P1 exopod of *Z. biarticulatus* and that of the genus *Perissoscope*. Itô did not assign his species to *Perissoscope* because it lacked the proximally-born inner seta on P1 exp-1 distinctive of this genus. Watkins (1987) remarked that *Zausodes* and *Perissoscope* are more closely related morphologically, ecologically and zoogeographically than either is to any other genus of the Harpacticidae. He suggested that the similar body shape between *Zausodes* and the other *Zausodinae* was a product of convergent evolution, particularly as the various body somites contribute differently to the overall teardrop shape, and similar convergences are found in *Harpacticus compressus* Frost, *Discoharpacticus mirabilis* Noodt and *Perissoscope biarticulatus* Watkins.

Preliminary phylogenetic analysis (Huys, unpubl.) supports a robust sistergroup relationship between *Perissoscope* and *Zausodes* sensu lato on the basis of the following synapomorphies:

1. strong sexual dimorphism in the shape of the rostrum;
2. antennule ♀ with fused segments 7 and 8 (representing ancestral segments XXIV and XXV) forming compound double segment (see below: character 1);
3. armature of P1 exp-3 consisting of 2–3 simple (unhinged) and 2 geniculate (hinged) claws (see below: character 8); confirmed by re-examination of the type material of *P. adiastaltus* Wells (BNHM 1967.7.11.5–6);
4. sexual dimorphism of P2 involving the loss of the inner distal seta of exp-3 in the male; this seta is generally reduced in length in other harpacticid genera such as *Harpacticus*, *Tigriopus* and *Paratigriopus* but is completely absent in *Zausodes* sensu lato and *Perissoscope*.

With the recent description of *P. biarticulatus* by Watkins (1987) the absence of the inner seta on P2–P4 exp-1 can no longer be regarded as a synapomorphy linking *Perissoscope* and *Zausodes*. The adhesive mucus strings produced by the caudal rami and the associated glands were first described for *Z. sextus* and *Z. septimus* by Lang (1965) and subsequently also reported for species of *Perissoscope* by Watkins (1987). This character is not unique to these two genera since a similar mucus apparatus has also been recorded in other representatives of the Harpacticidae (Watkins, 1987) and even outside this family (Huys, 1990).

Although the *Zaus-Zausopsis* clade is undoubtedly monophyletic, recognizing it as a distinct subfamily *Zausodinae* would relegate the Harpacticinae to a taxon of paraphyletic status. We recommend therefore to abandon Lang's (1944, 1948) subfamilial classification until a comprehensive phylogenetic analysis of the family is completed.

Morphological characters

(1) Segmentation ♀ antennule

The female antennule is primitively 9-segmented in the Harpacticidae with segments 7 and 8 representing ancestral segments XXIV and XXV, respectively. The homology of these segments is established by their posterior setae (Huys & Boxshall, 1991). This ancestral condition is found in the genera *Harpacticus*, *Zaus*, *Discoharpacticus*, *Tigriopus* and *Paratigriopus*. Within the former *Zausodes* complex the number of antennular segments ranges between 6 and 8. The 8-segmented state is derived by fusion of segments 7 and 8, forming a double segment in *Z. arenicolus*, *Z. septimus*, *A. biarticulatus* and the two species of *Mucropedia*. The origin of this compound segment is unequivocally established by the presence of

2 posterior setae. Comparison of ontogenetic studies of harpacticid genera possessing 9-segmented antennules such as *Tigriopus* (Itô, 1970) and *Harpacticus* (Itô, 1971, 1976; Itô & Fukuchi, 1978) indicates that the double segment is not the result of a failure in the separation of segments 7 and 8 at an earlier stage in ontogeny since both these segments are already expressed at copepodid I. The double segment is also found in all other *Zausodes* species (Table 1) in which the antennule is only 7- or 6-segmented. It is regarded here as a synapomorphy linking *Perissoscope* and the *Zausodes* complex.

A further derived state is found in the 3 Brazilian species (Jakobi, 1954), *N. sextus*, *N. schulenbergeri* and *N. areolatus* in which a triple segment is formed by incorporation of segment 6 into the double segment, producing a 7-segmented (or 6-segmented in *N. areolatus*) antennule. This condition has independently evolved in the genus *Perissoscope* (Wells, 1968). Our study has revealed a 6-segmented antennule in *N. areolatus* which represents an autapomorphy for this species. It has originated through fusion of segment 5 to the aesthetasc-bearing segment 4.

(2) Proximal elements ♀ antennule

The armature elements on the ♀ antennule are typically setiform in the great majority of the genera in the Harpacticidae. In some species of *Zausodes* sensu lato particular elements on the proximal segments are modified into stout, rigid spines which typically bear a subapical flagellum (Figs 8A; 14A). The position and number of these spines is identical in all species for which they have been recorded, i.e. two on segment 3 and one on segments 4 and 5 each. Two spines are found on segment 4 in *N. areolatus* as a result of secondary segmental fusion.

(3) Distal elements ♀ antennule

Some species of *Zausodes* sensu lato possess two large, conspicuous spines on segment 6 (or the homologous portion of segment 5 in the 6-segmented antennule of *N. areolatus*). These spines are typically unilaterally pinnate or pectinate (Figs 8A; 14A) and easy to discern without dissection. They are not found on the male antennules.

(4) Setal ornamentation ♀ antennule

Species of *Perissoscope* and *Zausodes* sensu lato typically have antennular setae which lack any form of ornamentation. Outgroup comparison with other harpacticid genera such as *Zaus* (Itô, 1980) and *Harpacticus* (e.g. Itô, 1976) suggests that this is the ancestral condition. In the type species *Z. arenicolus* (Fig. 2B) and *Z. septimus* (Lang, 1965; Mielke, 1990) the four proximal segments of the ♀ antennule bear pinnate setae, the plumosity being much more expressed in the latter. This modification is regarded here as apomorphic.

(5) Segmentation antennary exopod

Within the Harpacticidae the antennary exopod is 3-segmented only in *Tigriopus* and some species of *Perissoscope*. Comparison of setation patterns indicates that the 2-segmented condition is derived by fusion of the middle and distal exopod segments. This segmentation is found in most harpacticid genera such as *Harpacticus*, *Zaus*, *Zausopsis* and *Harpacticella*, and in three species of the former *Zausodes* complex (*biarticulatus*, *kirstenae*, *cookorum*). All other *Zausodes* species show the further derived 1-segmented state (Table 1), being the most reduced condition within the family.

(6) Armature antennary exopod

The maximum setation is found in *Harpacticus*, *Zaus* and *Zausopsis* which possess 2 lateral setae on exp-1 and 2 lateral plus 2 apical

Table 1 Segmentation of ♀ antennule (A1) and antennary exopod (A2), armature formula of antennary exopod and swimming legs P2–P4 in *Perissocope* (2 species) and 12 species of the *Zausodes* complex. The swimming leg armature formulae of *Z. cinctus* Krishnaswamy and *P. adiastaltus* Wells have been corrected (see text).

	Segmentation			Armature			
	A1	A2	A2	P2	P3	P4	
<i>arenicolus</i>	8	1	2	0.1.223	0.1.221	0.1.323	0.1.323
<i>areolatus</i>	6	1	2	0.1.223	0.1.221	0.1.323	0.1.323
<i>biarticulatus</i>	8	2	(2+2)	0.1.223	0.1.221	0.1.323	0.1.323
<i>cinctus</i>	7	1	2	0.1.223	0.1.221	0.1.323	0.1.323
<i>cookorum</i>	[♀]	8	2	(2+2)	0.1.223	0.1.221	0.1.322
	[♂]						0.1.221
<i>kirstenae</i>	[♀]	8	2	(2+2)	0.1.223	0.1.221	0.1.322
	[♂]						0.1.323
<i>limigenus</i>	7	1	2	0.1.223	0.1.121	0.1.323	0.1.323
<i>paranaguaensis</i>	7	1	2	0.1.223	0.1.120	0.1.323	0.1.323
<i>septimus</i>	8	1	2	0.1.223	0.1.221	0.1.323	0.1.323
<i>sextus</i>	7	1	2	0.1.223	0.1.221	0.1.323	0.1.323
<i>shulenbergeri</i>	7	1	2	0.1.223	0.1.121	0.1.323	0.1.323
<i>stammeri</i>	7	1	2	0.1.223	0.1.121	0.1.323	0.1.323
<i>Perissocope</i>							
<i>adiastaltus</i>	7	3	(2+0+3)	0.1.223*	0.1.221	0.1.323	0.1.323
<i>biarticulatus</i>	8	3	(1+0+3)	1.1.223	0.1.221	1.1.323	1.1.322
							1.1.221

* Wells (1968) figured P2 exp-3 with formula 323; this is clearly based on an aberrant specimen since no extant harpacticoid has more than 7 elements on this segment (Huys & Boxshall, 1991; also confirmed by re-examination of other type material).

setae on exp-2. Comparison with the 3-segmented exopod in *Tigriopus* suggests that the proximal lateral seta on exp-2 in these genera originates from the incorporated middle segment and therefore the ancestral setal formula must have been [2,1,3]. In *Perissocope* the lateral seta on exp-2 is lost resulting in a [2,0,3] formula in *P. adiastaltus* Wells or [1,0,3] in *P. biarticulatus* Watkins. Further setal reduction has occurred in the *Zausodes* complex where only 2 setae are retained on the distal segment in the most primitive species (*biarticulatus*, *kirstenae*, *cookorum*), or secondarily, the exopod became an unsegmented bisetose ramus (all other species).

(7) Armature praecoxal endite maxilla

Some species of *Perissocope* have 5 elements on the praecoxal endite of the maxilla (Huys *et al.*, 1996; Fig. 106F) which is the highest number recorded in any member of the Harpacticidae. This number is reduced to four (state 1) or three setae (state 2) in the *Zausodes* complex. Itô (1979) recorded variability in the maxilla of *Z. biarticulatus* and regarded the 3-setae condition as the typical one. The ‘atypical’ maxilla illustrated in his Fig. 3–1 shows 4 elements arranged in the same pattern as found in *Z. arenicolus* (Fig. 3B) and *Z. septimus* (Mielke, 1990: Abb. 3A). On the basis of this similarity we have scored state 1 for *Z. biarticulatus*. Lang (1965) showed only 2 setae on this endite but we suspect that the third one was overlooked and have given this species a score 2 accordingly (Table 3).

(8) Armature P1 exp-3

The distal exopod segment of P1 is small or vestigial in the Harpacticidae and typically embedded in the distal margin of the middle elongate segment. Huys *et al.* (1996) described the basic armature of this segment as four unhinged claws, 1 hinged claw and a seta, but careful re-examination of a range of genera revealed that the seta in reality belongs to the middle exopod segment. This seta is often small (e.g. Fig. 5C) and sited at the distal inner corner of exp-2. Huys *et al.*’s misconception stems from observations of *Harpacticus* and *Zaus* in which the distal segment is largely incorporated in the middle one. In other genera such as *Harpacticella* and *Tigriopus* the distal segment is well delimited showing the real

origin of the inner seta (Itô, 1970, 1977; Itô & Kikuchi, 1977). Both *Perissocope* and the *Zausodes* complex deviate from the normal armature pattern by the presence of two hinged (geniculate) claws (see above). The modification of one of the simple claws into a second geniculate one is a synapomorphy for these taxa. Species of the *Zausodes* complex have lost one of the simple claws, retaining only four elements on exp-3 (2 geniculate and 2 simple claws).

(9) Armature P1 enp-1

Harpacticidae typically possess a well developed inner seta on the proximal endopod segment of P1. The exceptions to this rule are the species belonging to the *Zausodes* complex which have secondarily lost this seta.

(10) Armature P2 enp-3

Most Harpacticidae have 2 inner setae on the distal endopod segment of P2. Some species within the *Zausodes* complex possess only 1 seta on this segment (Fig. 15A; Table 1). This reduction has evolved convergently in other genera such as *Harpacticus* (e.g. *H. componyx*) and *Tigriopus*.

(11) Armature P3 enp-2

The inner seta on the middle endopod segment of P3 is present in most harpacticid genera, including *Perissocope*. Within the *Zausodes* complex, however, this seta is commonly lost and is retained only in *Z. biarticulatus* (and the imperfectly described *Z. cinctus* – see below).

(12) Armature P3 enp-3

Species of *Perissocope* and most other genera of the family possess 3 inner setae on the distal endopod segment of P3. Various reductions occur in the more advanced genera *Tigriopus*, *Paratigriopus* and *Discoharpacticus*. All species of the *Zausodes* complex invariably have 2 inner setae on this segment.

(13) Armature P4 exp-3

Sexual dimorphism in the number of armature elements on the P4 exopod is extremely rare within the Harpacticoida. In some species

Table 2 Characters used in phylogenetic analysis. Apomorphic character states are referred to in square brackets. Characters 5–7 are multistate characters.

1	Antennule ♀ 8-segmented [7-segmented, segments 6 and 7 fused]
2	Antennule ♀ with only setiform elements on segments 3, 4 and 5 [segment 3 with 2 and segments 4–5 with 1 strong, modified spine]
3	Antennule ♀ segment 6 (or homologous portion in 6- or 7-segmented antennule) without enlarged spines [with 2 enlarged pectinate or pinnate spines]
4	Antennule ♀ with all elements naked (except for pinnate spines referred to in character 3) [with pinnate or plumose setae on segments 1–6]
5	Antennary exopod 3-segmented [state 1: 2-segmented; state 2: 1-segmented]
6	Antennary exopod with total of 5 setae (2 on exp-1, 3 on exp-3; exopod 3-segmented) [state 1: 2 on exp-1, 2 on exp-2 and exopod 2-segmented; state 2: total of 2 setae on single segment]
7	Maxilla with 5 setae on praecoxal endite [state 1: 4 setae; state 2: 3 setae]
8	P1 exp-3 with 2 geniculate (hinged) and 3 simple claws [with 2 geniculate and 2 simple claws]
9	P1 enp-1 with long inner seta [without]
10	P2 enp-3 with 2 inner setae [with 1 inner seta]
11	P3 enp-2 with inner seta [without]
12	P3 enp-3 with 3 inner setae [with 2 inner setae]
13	P4 exp-3 with 3 outer spines in ♀ [with 2 outer spines in ♀, 3 in ♂]
14	P4 endopod 3-segmented [2-segmented; enp-2 and -3 fused]
15	P4 enp-2 (or homologous portion in 2-segmented endopod) with inner seta [without inner seta]
16	P4 enp-3 (or homologous portion in 2-segmented endopod) with 2 inner setae [with 1 inner seta]
17	P5 exopod oval or elongate in both sexes [round]
18	P5 ♀ endopodal lobe expressed [completely lost]
19	P5 ♀ endopodal lobe inner seta not distinctly shorter than other endopodal elements [rudimentary]
20	P5 ♀ endopodal lobe 3rd and 4th setae well developed [much shorter than others]
21	Antennule ♂ segment 3 without transformed elements [with modified spine]
22	P2 enp-2 ♂ with apophysis [secondarily lost]
23	P2 enp-2 ♂ inner element setiform, not sexually dimorphic [modified into stout spine, distinctly shorter than in ♀]
24	P2 enp-3 outer spine articulating with segment [fused to segment]
25	P3 enp-2 ♂ outer distal corner not attenuated [attenuated]

Table 3 Character data matrix. Characters listed in Table 2 are scored using the multistate system: 0 = ancestral (plesiomorphic) state, 1 = derived (apomorphic) state, 2 = further derived state, ? = missing data, indicating that the character state is either unknown or unconfirmed.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>arenicolus</i>	0	0	0	1	2	2	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	
<i>areolatus</i>	1	1	1	0	2	2	2	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	
<i>biarticulatus</i>	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	0	1	0	
<i>cookorum</i>	0	0	0	0	1	1	1	1	0	1	1	1	1	1	0	0	0	1	1	0	0	1	1	1	
<i>kirstenae</i>	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	0	0	1	1	0	0	1	1	1	
<i>limigenus</i>	1	1	1	?	2	2	?	1	1	1	1	1	0	1	1	1	0	0	0	?	?	?	?	?	
<i>paranaguaensis</i>	1	1	1	?	2	2	?	1	1	1	1	1	0	1	1	1	1	0	0	?	?	?	?	?	
<i>septimus</i>	0	0	0	1	2	2	1	1	0	1	1	0	0	1	1	1	0	0	0	1	0	1	0	0	
<i>sextus</i>	1	1	1	0	2	2	2	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	
<i>shulenbergeri</i>	1	1	1	0	2	2	2	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1	0	0	
<i>stammeri</i>	1	1	1	?	2	2	?	1	1	1	1	1	0	1	1	1	1	0	0	?	?	?	?	?	
<i>PERISSOCOPE</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>cinctus</i>	1	0	0	0	2	2	?	1	1	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	

of the Thompsonulidae (Huys & Gee, 1990) and Tetragonicitipitidae (Kunz, 1984) sexual dimorphism involves the loss of elements in the male, whereas in species of *Huntemannia* Poppe an increase in the number of elements has been reported (Wilson, 1958; Geddes, 1968b). Two new species from the Gulf of Mexico (*kirstenae*, *cookorum*) show 2 outer spines on the distal exopod segment of P4 in the female and a supernumerary spine in the male. All other species of the *Zausodes* complex possess 3 spines in both sexes.

(14) Segmentation P4 endopod

Only three species of the *Zausodes* complex (i.e. *arenicolus*, *kirstenae* and *cinctus*) have retained the 3-segmented condition of the P4 endopod. In all other species the middle and distal segments have failed to separate, resulting in a 2-segmented ramus. Lang (1965) refused to split up *Zausodes* on the basis of P4 endopod segmentation since for many other characters close congruence was found between species with different segmentation. Lang assumed that the 2-

segmented state had arisen convergently and pointed out that the original division of the distal segment in *Z. sextus* is still indicated by a dentiform notch along the outer margin. An incomplete surface suture was also found in *Z. areolatus* (Fig. 11C), suggesting that the P4 endopod segmentation is probably an evolutionary labile character.

(15) Armature P4 enp-2

Most harpacticid genera displaying a 3-segmented P4 endopod possess an inner seta on the middle segment. This seta has been lost in the *Zausodes* complex (except *Z. cinctus*), including the two species in which the middle segment is still separated (*kirstenae*, *arenicolus*).

(16) Armature P4 enp-3

The maximum number of inner setae on the distal (enp-3) endopod segment of P4 in any species of the Harpacticidae is two. This number is found in most members of the family, including some (but

not all) species of *Perissocope* such as *P. biarticulatus*. Within the *Zausodes* complex 2 setae are found in only four species (Table 1), however in both *biarticulatus* and *cookorum* the distal segment represents the fused enp-2 and -3, obscuring the origin of the proximal inner seta. Comparison with the closely related *kirstenae*, in which all segments are expressed, suggests that both inner setae are derived from enp-3.

(17) Shape P5 exopod of both sexes

The P5 exopod is usually oval or elongate in both sexes. In one species group of the *Zausodes* complex the exopod is distinctly round (e.g. Figs 15D, 18D) which by outgroup comparison with *Perissocope* and other genera is regarded here as the apomorphic condition.

(18) Shape P5 ♀ endopodal lobe

The endopodal lobe is well developed in the majority of female harpacticids, including most members of the *Zausodes* complex. In four species (*biarticulatus*, *kirstenae*, *cookorum*, *cinctus*) the whole baseoendopod is modified, forming a transversely elongated plate, and the endopodal lobe is no longer expressed (Figs 23B; 30C).

(19–20) Armature P5 ♀ endopodal lobe

Species belonging to *Perissocope* and the *Zausodes* complex typically have 5 well developed setae on the P5 endopodal lobe of the female. In some species of the latter particular elements have undergone secondary reduction in size. In the *cookorum*-*kirstenae*-*biarticulatus* group the innermost seta is rudimentary and sited at the extreme distal corner near the articulation with the exopod (Figs 23B, 30C; character 19 in Table 3). Further reduction has occurred in *biarticulatus* where the three innermost setae are completely vestigial (Itô, 1979). In the type species *Z. arenicolus* the 3rd and 4th setae (counted from the innermost according to Huys *et al.* (1996)) are very reduced and the innermost one is well developed. This reduction is treated separately as character 20 in Table 3 and scored as state 1 in both *arenicolus* and *septimus*. In the latter one of the smaller setae is lost, retaining only 4 elements on the endopodal lobe (Lang, 1965; Mielke, 1990). The reduction of setae 3 and 4 in *biarticulatus* is regarded here as a further derived state of character 19 and not as the apomorphic state of character 20.

(21) Armature antennule ♂

Male antennules in the Harpacticidae are of the subchirocer or chirocer type. Armature elements are typically modified on the segments located either side of the geniculation. In one group of the *Zausodes* complex the male antennule also possesses a modified element on segment 3. It is represented by a strong spine which is situated dorsally near the distal margin of the segment (Figs 12F, 18A).

(22–23) Modification P2 enp-2♂

The male P2 endopod is of high significance in understanding the phylogeny of the Harpacticidae (Itô, 1984). Many genera possess an outer spinous apophysis on the middle endopod segment which attains its maximum size in *Harpacticus* and *Discoharpacticus*. Analysis of the phylogenetic relationships within the family (Huys, unpubl.) suggests that this apophysis has become gradually smaller during harpacticid evolution and was lost independently in *Paratigriopus*, *Harpacticella* and *Zaus-Zausopsis*. A similar regressive evolution has also been documented in the Paranannopidae for a similar apophysis on the male P2 endopod (e.g. Gee & Huys, 1991; Huys & Gee, 1993, 1996). Within the *Perissocope*-‘*Zausodes*’ lineage the apophysis is clearly in a state of reduction. The genus

Perissocope combines both species with a slender apophysis (*P. biarticulatus*, *P. exiguum*, *P. bayeri*) and species without such an uncinate process (*P. adiastaltus*). Within the former *Zausodes* complex only the type species *Z. arenicolus* possesses a short spinous outgrowth on P2 enp-2 (Fig. 7E) whereas all other species have lost the apophysis completely (Figs 12D, 17C, 22D).

In both *kirstenae* and *cookorum* the inner element of P2 enp-2 is sexually dimorphic, being setiform in the ♀ and modified into a short stout spine in the ♂ (character 23 in Table 3; Figs 22D, 29A).

(24) Modification P2 enp-3♂

The outer spine on the distal endopod segment of the male P2 is frequently modified in the Harpacticidae. In male *Harpacticus* the outer spine is usually lost at the final moult or not formed at all in any male copepodid instar (Itô, 1984). In some species such as *H. furcatus* Lang the outer spine is represented by a rudimentary setule (Itô & Fukuchi, 1978). In other genera such as *Tigriopus*, *Paratigriopus* and *Zaus* the outer spine is not sexually dimorphic and articulating with the segment. A different modification is found in male *Perissocope* where the outer spine is completely integrated into the distal segment, forming a long, slender apophysis (e.g. Vervoort, 1964; Pallares, 1975; Watkins, 1987; Wells, 1968). A similar apophysis was found by Itô (1979) in *Z. biarticulatus* and in two new species (*kirstenae*, *cookorum*) described here. In the latter the apophysis is represented by a spinous process which is minutely pectinate at the inner subapical margin and about equal in length to the outer spine in the female (Figs 22D, 29A).

(25) Modification P3 enp-2♂

Distinct sexual dimorphism on the P3 endopod is rare in the Harpacticidae. Differences in surface ornamentation between the sexes are occasionally found in *Harpacticus* (Itô, 1976; Itô & Fukuchi, 1978) and in species of the *Zausodes* complex (*shulenbergeri*, *kirstenae*), however, these have not been included in the analysis. A more pronounced modification involves the formation of a mucroniform process at the outer distal corner of the middle segment. This is found in the genus *Perissocope* and in two closely related species of the *Zausodes* complex (*kirstenae*, *cookorum*) (Figs 22E, 29D).

Data matrix and analysis

In order to resolve the relationships within the *Zausodes* complex the analysis was executed at the species level. The characters used in the analysis of phylogenetic relationships between *Perissocope* and the 12 species of the *Zausodes* complex are listed in Table 2. The character states are explained inside square brackets using the multistate system: 0 = the ancestral state, 1 = the derived state, 2 = a further derived state. The scores for each character and taxon are compiled in matrix format in Table 3. A question mark indicates missing data, either because the appendage or structure is unknown in that species (certain sexually dimorphic characters could not be scored because only one sex is known) or because it was impossible to score the character accurately due to the lack of detail in the original descriptions (cf. Jakobi, 1954). *Z. cinctus* Krishnaswamy was excluded from the analysis. Its status is discussed below.

RESULTS AND DISCUSSION

Two most parsimonious trees were obtained with tree-length 36 and consistency index 0.778 (Fig. 33). Both trees differ only in the position of *Z. septimus* which in tree A forms a monophyletic group

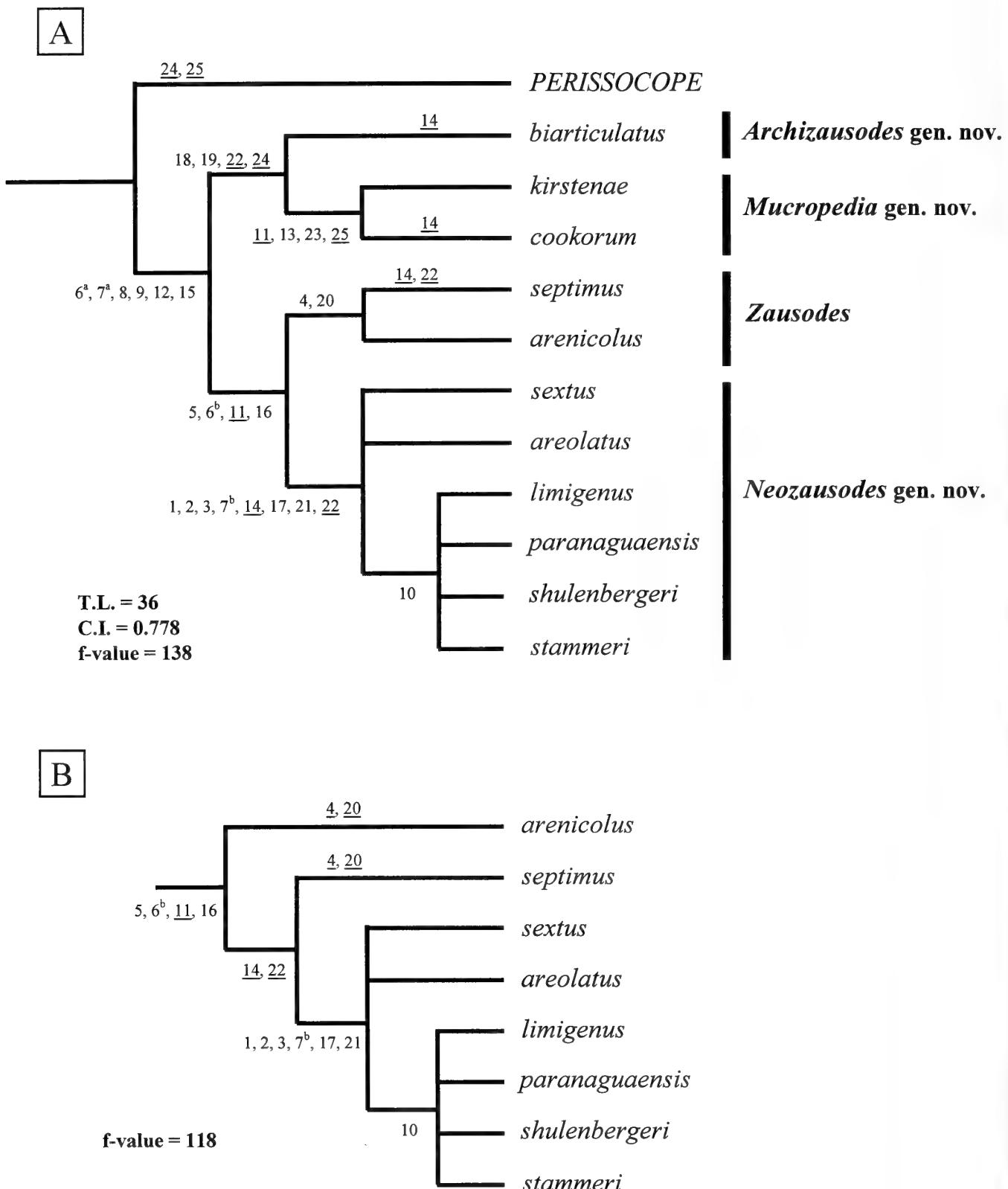


Fig. 33 Optimal trees depicting relationships between species of the *Zausodes* complex and the genus *Perissoscope*. Numbers refer to apomorphic states of characters listed in Table 2 [underlined numbers refer to convergences, superscript letters indicate multistate characters]. T.L. = tree-length; C.I. = consistency index.

with *Z. arenicolus*, whereas in tree B it occupies a transitional position between the type species and the other *Zausodes* species. Tree B has a lower f-value (118) than tree A (138), however, we have selected the latter as the optimal one on account of the lower number of convergences. In tree A *Z. septimus* and *Z. arenicolus* are clustered on the basis of two apomorphies which are unique to these two species (characters 4 and 20). This grouping is at the expense of introducing convergences for characters 14 and 22, however, both these characters already show convergence in other clades (Fig. 33A) and are known to be evolutionary labile. The justification for grouping *Z. septimus* with the other *Zausodes* species in tree B is based solely on the convergent evolution of characters 14 and 22, thereby causing additional homoplasies for characters 4 and 20.

The monophyly of the *Zausodes* complex and its sistergroup relationship to *Perissoscope* are confirmed. The complex is divided in two lineages by a strongly supported basal dichotomy and each lineage is composed of two clades.

The *biarticulatus-kirstenae-cookorum* lineage is supported by leg 5 characters such as the loss of the endopodal lobe and the reduction of the innermost seta of the baseoendopod. Additional apomorphies are the modification of the distal outer spine on the male P2 endopod and the sexual dimorphism on the P3 endopod. A peculiar character shared by these species (but not used in the analysis) is the presence of a well developed hyaline frill on the distal endopod segment of P1. Under the traditional light microscope this frill resembles a tuft or fan of spinules sited at the distal outer corner of enp-2 (Figs 22C, 29E). All three species have retained the primitive segmentation and setation of the antennary exopod. Within this lineage *Z. biarticulatus* occupies the most primitive position since it is the only species which has retained the inner seta on P3 enp-2. The other species (*cookorum*, *kirstenae*) are clustered on the basis of their unique sexual dimorphism on the P2 endopod, P3 endopod and P4 exopod.

The monophyly of the second lineage which includes all other species is supported by the 1-segmented antennary exopod bearing only 2 setae and the reduced armature on the P4 endopod. A basal dichotomy divides the lineage into two distinct clades, the *arenicolus*-clade and the *sextus*-clade. The former accommodates the type species and *Z. septimus* and is characterized by the presence of ornate setae on the ♀ antennule and by the reduction of particular setae on the ♀ P5 baseoendopod. Both species have retained primitive antennule characters such as the 8-segmented condition in the ♀ and the complete absence of modified elements in both sexes. The *sextus*-clade, encompassing 6 closely related species, is extremely well supported but largely unresolved. This is partly due to the deficient descriptions of the Brazilian species (*limigenus*, *stammeri*, *paranaguaensis*) for which it has proven impossible to score all characters (Table 3). The clade is defined by the 7(or 6 in *areolatus*)-segmented ♀ antennule, the presence of modified spines in both proximal and distal regions of the ♀ antennule and on segment 3 of the ♂ antennule, the reduced armature on the maxillary praecoxal endite and the round shape of the P5 exopod in both sexes. A subgroup, combining *shulenbergeri* and Jakobi's (1954) species, can be recognized within this clade and is characterized by the presence of only 1 inner seta on P2 enp-3.

Itô (1979) already remarked that *Z. biarticulatus* occupied a separate taxonomic position within *Zausodes* and highlighted particular similarities with the genus *Perissoscope*. Lang (1965) on the other hand favoured a subdivision of the genus *Zausodes* but was reluctant to do so on the basis of P4 endopod segmentation. Our analysis has revealed marked intrageneric differences in the sexual dimorphism of all three swimming legs (P2–P4), the setation and

armature of the antennary exopod, and the form and modification of antennular elements in both sexes. Such variability has not been recorded for any of the other 8 genera in the family, suggesting that the *Zausodes* complex combines distinct lineages which – in accord with the generic concept currently applied in the Harpacticidae – would deserve generic status. The genus *Zausodes* is therefore redefined to include only *Z. arenicolus* and *Z. septimus*, and three new genera (*Archizausodes* gen. nov., *Mucropedia* gen. nov. and *Neozausodes* gen. nov.) are proposed, reflecting the basic topology illustrated in Fig. 33A.

Status of *Zausodes cinctus* Krishnaswamy, 1954

The taxonomic position of this species from off the Madras coast (India) is enigmatic since Krishnaswamy's (1954) description is erroneous in many aspects. We attempted but were unable to obtain the type specimens from the Zoological Survey of India in Calcutta. The strongly elongated P5 exopod is unique within *Zausodes* sensu lato and leaves little doubt that *Z. cinctus* is a distinct species. However, the numerous deficiencies in the original figures make it impossible to allocate this species to one of the four genera recognized herein. For example, Krishnaswamy (1954) claims that the P1 exopod is only 2-segmented and sexually dimorphic, the male having only 2 claws and 1 seta on the distal segment and no outer seta (corresponding to exp-2). The endopod of this leg is reminiscent of the laophontid type, bearing only one strong claw on the distal segment. There is no doubt that the author has overlooked elements on both rami and that his report of sexual dimorphism is based on this oversight. Similarly, there is considerable confusion over the armature formula of the endopods of P2–P4. According to Krishnaswamy the distal endopod segment of P2–P4 has 1 terminal and 3 inner setae which Lang (1965) translates as a [211] formula, implying that an outer spine is present. The latter is invariably short in Harpacticidae, however, Krishnaswamy's figures show only a long plumose seta which is outwardly directed. We speculate that this unusual orientation of the outer apical seta (perhaps as a result of imperfect mounting) has obscured the outer spine (cf. Itô's (1979) drawings of *A. biarticulatus*) and that the armature formula of P2–P4 enp-3 is more likely [221] as in *Archizausodes* and *Mucropedia*. If this assumption is correct then *Z. cinctus* displays the most primitive swimming leg armature within *Zausodes* sensu lato since no other species possesses an inner seta on P4 enp-2 (and *A. biarticulatus* being the only other species to exhibit an inner seta on P3 enp-2). In this context we point out the possible homology between the latter seta and the proximal inner seta of P4 enp-2 in *A. biarticulatus* which we – by reference to the 1.0.221 pattern in closely related *M. kirstenae* (Table 1) – have interpreted as originating from enp-3.

Another remarkable feature is the presence of only 4 elements on the ♀ P5 exopod. Krishnaswamy's illustration shows a distinct gap between the proximal and distal outer spine which corresponds with the position of the vestigial seta on the P5 of *A. biarticulatus* (cf. Itô, 1979: Fig. 5–1). It is conceivable that a similarly reduced seta is present in *Z. cinctus*. Both species, coincidentally the only Asian representatives of the *Zausodes* complex, also share the absence of the endopodal lobe and show a similar arrangement of the endopodal setae (with *Z. cinctus* having an additional long seta).

The male P2 endopod of *Z. cinctus* was neither described nor illustrated by Krishnaswamy (1954). Sexual dimorphism in the P2 endopod is always present in the *Zausodes* complex, so it is conceivable that it was overlooked. Pending the re-examination of Krishnaswamy's types or topotype material we rank *Z. cinctus* as *species incertae sedis* in the Harpacticidae.

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***Nybelinia southwelli* sp. nov. (Cestoda, Trypanorhyncha) with the re-description of *N. perideraeus* (Shipley & Hornell, 1906) and synonymy of *N. herdmani* (Shipley & Hornell, 1906) with *Kotorella pronosoma* (Stossich, 1901)**

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SYNOPSIS. During a study of *Nybelinia* material deposited at The Natural History Museum, London, *Nybelinia southwelli* sp. nov. was discovered amongst material identified and described as *Tetrarhynchus perideraeus* Shipley & Hornell, 1906 from *Rhina aenyllostoma* and *Nebrius ferrugineus* from Sri Lanka. The new species belongs to the subgroup IIBa of Palm *et al.* (1997), which includes species having a homeoacanthous heteromorphous metabasal armature and a characteristic basal armature where the basal hooks are smaller or equal in size to the metabasal hooks. It can easily be distinguished from all other members of this group by having characteristic rose-thorn shaped metabasal and slender basal hooks. The type material of *Nybelinia perideraeus* (Shipley & Hornell, 1906) was borrowed from the Natural History Museum, Vienna, for comparison, and is re-described. *N. dakari* Dollfus, 1960 is considered synonymous with *N. perideraeus*. *Nybelinia herdmani* (Shipley & Hornell, 1906), also placed in the subgroup IIBa by Palm *et al.* (1997), is considered synonymous with *Kotorella pronosoma* (Stossich, 1901) Euzet & Radujkovic, 1989. The subgroupings of *Nybelinia* species based on the species specific tentacular armature appear to be useful for further taxonomic studies within the genus.

INTRODUCTION

Trypanorhynch cestodes are common parasites of marine elasmobranchs, where they mature in the stomach or the spiral valve. The plerocercoids are parasitic in many teleosts and a variety of invertebrates while the first intermediate hosts are crustaceans. Among trypanorhynch cestodes, *Nybelinia* Poche, 1926 is the largest genus. Palm *et al.* (1997) listed 43 adequately described species while leaving 4 species of uncertain status, and Jones & Beveridge (1998) added *N. queenslandensis*. Vijayalakshmi *et al.* (1996) described *Tentacularia scoliodoni* on the basis of the tentacular armature, not considering the most recent generic definitions of *Tentacularia* and *Nybelinia* in the key of Campbell & Beveridge (1994). The species strongly resembles *N. indica* Chandra, 1986 and *N. africana* Dollfus, 1960, and should be treated as species of uncertain status pending on examination of further material. Thus, with a total of 44 adequately described species, the genus *Nybelinia* currently comprises the most species-rich genus within the order Trypanorhyncha.

One of the biggest problems for taxonomic work within the genus, apart from poor original descriptions, remains the lack of information on material available in museum collections for comparative morphological studies. Many species have a similar scolex morphology and tentacular armature. Additionally, several species descriptions are based on single specimens and data on intraspecific

variability are scarce. Studies of *Nybelinia* deposited in collections are needed to determine validity as well as for re-descriptions.

During a study on *Nybelinia* material deposited at the British Museum, Natural History, slides labelled and described as *Tetrarhynchus perideraeus* Shipley & Hornell, 1906 from the T. Southwell collection (Southwell, 1929a, p. 257–259) appeared to bear a species different to that indicated. The present study was carried out to clarify the identity of this material. The type material of *Nybelinia perideraeus* was borrowed from the Natural History Museum, Vienna, for comparison, and re-description. Beside this, the taxonomic position of *N. herdmani* (Shipley & Hornell, 1906) is clarified.

MATERIAL AND METHODS

Standard measurements and drawings of the scoleces of *Nybelinia* specimens deposited in the Parasitic Worms Division, The Natural History Museum London (BMNH), were made using a Leitz Wetzlar Dialux 20 microscope with an ocular micrometer. The type specimens of *Nybelinia perideraeus* and *N. herdmani* were borrowed from the collection of the Naturhistorisches Museum Wien (VNMH) and examined with a Leitz Wetzlar Orthoplan microscope. Drawings were made using a Leitz Wetzlar Dialux 22 microscope with a drawing tube.

The following measurements were taken: Scolex length (SL), scolex width at level of pars bothridialis (SW), pars bothridialis (pbo), pars vaginalis (pv), pars bulbosa (pb), pars postbulbosa (ppb), velum (vel), appendix (app), bulb length (BL), bulb width (BW), bulb ratio (BR), proportions of pbo/pv/pb (SP), tentacle width (TW), and tentacle sheath width (TSW). If possible, the tentacle length (TL) was estimated. Additionally, the tentacular armature was described as follows: armature homeomorphous or heteromorphous, hooks per half spiral row (hsr), total hook length (L) and the total length of the base (B).

All measurements are given in micrometers unless otherwise indicated. Illustrations are provided where useful, otherwise the reader is referred to illustrations of other authors. The classification follows that of Palm (1995, 1997) and the orientation of the tentacular surfaces follows that of Campbell & Beveridge (1994).

RESULTS

The comparison of *Tetrarhynchus perideraeus* Shipley & Hornell, 1906, BMNH 1977.11.4.7–9, 1977.11.11.38 from the Southwell collection with the co-type material of *T. perideraeus* from the VNHM (2109, 2111) revealed differences. The BMNH material corresponds neither with the co-types from the VNHM nor with specimens of *T. perideraeus* as re-described by Dollfus (1942, Figs 98–100). Similarly, the type material of *T. perideraeus* from the VNHM clearly differs from the specimens described by Dollfus (1942). Thus, the material deposited and described above belongs to three different *Nybelinia* species.

In the following, *Nybelinia perideraeus* (Shipley & Hornell, 1906) is re-described and the material collected by T. Southwell and deposited in the BMNH, which does not fit in any of the currently accepted species (Palm *et al.*, 1997), is described as *N. southwelli* sp. nov. Another species deposited in the VNHM, *Tetrarhynchus herdmani* (Shipley & Hornell, 1906), can be considered synonymous with *Kotorella pronosoma* (Stossich, 1901) Euzet & Radujkovic, 1989.

Superfamily TENTACULARIOIDEA Poche, 1926

Family TENTACULARIIDAE Poche, 1926

Genus NYBELINIA Poche, 1926

***Nybelinia southwelli* sp. nov.** (Figs 1–3c)

SYNONYMY.

N. perideraeus (Shipley & Hornell, 1906) of Southwell (1924, 1929a, b, 1930)

MATERIAL DESCRIBED. Holotype, BMNH 1977.11.4.7, J. Pearson leg., 30.9.1925, 1 adult from *Rhina ancylostoma* Bloch & Schneider, 1801 (=*Rhynchobatus ancylostomus*) Sri Lanka (Ceylon); Paratype, BMNH 1977.11.4.8–9, J. Pearson leg., 30.09.1925, 1 adult from *Nebrius ferrugineus* (Lesson, 1830) (=*Ginglymostoma concolor*), Sri Lanka. Other material: BMNH 1977.11.4.8–9 (2 slides) and BMNH 1977.11.11.38.

DESCRIPTION. With the characters of the genus *Nybelinia*: The scolex (BMNH 1977–11.4.8–9, Fig. 28B in Southwell, 1929a; BMNH 1977.11.11.38, see Fig. 1) is craspedote with a total length (with velum) of 1701/holotype (1739/paratype). The length of the bothridia is more than half the scolex length, the width at the pars

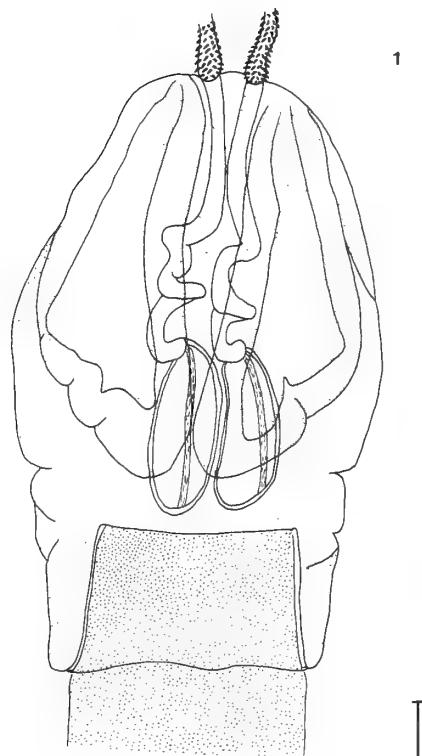


Fig. 1 Scolex of *Nybelinia southwelli* sp. nov. from *Nebrius ferrugineus*. Scale bar=150 µm.

bothridialis is 945 (1134); pbo=1078 (1058), pv=982 (926), pb=485 (415), ppb=56 (38), vel=298 (420), BL=474 (404), BW=166 (185), BR=2.9:1 (2.2:1), SP=2.2:2:1 (2.5:2.2:1). The tentacles are long and slender and diminish in size towards the tip; TW basal=46–51 (51–56), TW metabasal 33–38. A basal tentacular swelling is not present. The tentacle sheaths are sinuous or spirally coiled; TSW 66–70 (51–56). Prebulbular organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, heteromorphous with a characteristic basal armature consisting of 13–14 rows of homeomorphous hooks (Figs 2a, c(i)). The number of hooks per half spiral diminishes towards the apical part of the tentacles: hsr=6 (basal), hsr=4–5 (apical). The massive hooks of the metabasal (Figs 2b, c(ii)) and apical (Figs 2b, c(iii)) armature are different in shape and size on bothridial and antithothridial tentacle surfaces. The metabasal tentacular armature on the bothridial surface consists of strongly recurved solid hooks with a large base; L=17–18 (13–15), B=14–16 (10–12). On the antithothridial surface, the hooks are more slender and slightly curved with a stout base; L=20–22 (15–18), B=12–14 (8–9). The basal armature is homeomorphous, basal hooks with a stout base, a slender shaft, and strongly recurved at the tip (L=18–20 (14–16), B=7–8 (6–7)) (Figs 2a, c(i)). The first basal hooks are smaller than those of the remaining basal armature.

The morphology of the mature and gravid segments of *N. southwelli* sp. nov. is given in Southwell (1929a, Figs 28E–F), a description and measurements of the proglottids is given in Southwell (1929a, p. 259). The morphology of the strobila and mature and gravid proglottids of BMNH 1977.11.11.38 is given on Figs 3a–c. *N. southwelli* sp. nov. has a long acraspedote strobila of more than 232 proglottids (BMNH 1977.11.4.8–9, strobila not complete), which

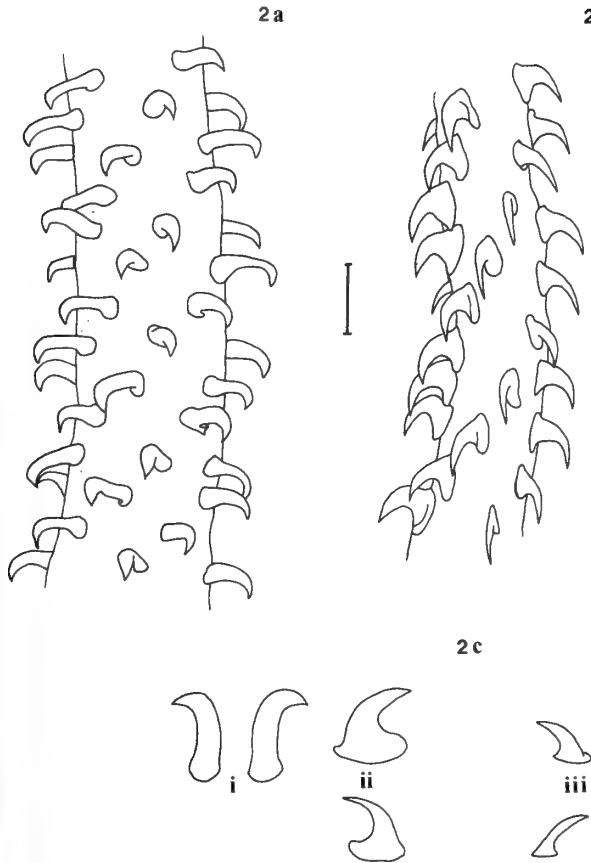


Fig. 2a–c *Nybelinia southwelli* sp. nov. a. homeomorphous basal tentacular armature, external surface. b. metabasal tentacular armature, external surface. c. basal (i), metabasal (ii) and apical (iii) tentacular hooks. Scale bar=20 µm.

are wider than long and have distinct convex margins (Fig. 3a). The size of the proglottids is similar along a large part of the strobila (around 130th proglottid: 800–870 × 260–300, last proglottids: 900–970 × 300–370). The genital atrium is ventrosubmarginal in about the middle of the proglottids and alternates irregularly. The cirrus sac is elongate, large, directed anteromedially from the genital atrium and the sac is thin-walled (Figs 3b–c). The cirrus is unarmed, coiled within the sac and an internal seminal vesicle was not seen; external seminal vesicle absent. Testes arranged in double layer, number 70–80, ovoid, 25–42 in diameter, encircle the female genital complex, and some testes are present anterior to the cirrus sac. Vagina not seen. Ovary bilobed, 130–160 wide × 80–105 long (BMNH 1977.11.4.8–9). Gravid segments with vitelline follicles of 15–20 in diameter, uterus extending over most of the proglottids. Other details of the female genital complex not seen.

ETYMOLOGY. The new species was named after T. Southwell, in whose collection the present specimens were found.

REMARKS.

Southwell (1924, 1929a, 1930) gave a first description of *N. southwelli* sp. nov. but identified the specimens as *N. perideraeus* Shipley & Hornell, 1906. His scolex measurements lie within the same range (Southwell, 1929a, p. 257–258; 1930, p. 84–86), and the illustrations of the tentacular armature are similar to Figs 2a–c. Fig. 28d in Southwell (1929a) as well as Fig. 16d in Southwell (1930) illustrate the slender, strongly recurved hooks of the basal tentacular

armature (Fig. 2a), and Southwell's Figs (28c and 16c) illustrate the metabasal armature with the rose-thorn shaped hooks (Fig. 2b). However, in contrast to his drawings, Southwell wrongly interpreted the tentacular hooks as being uniform in size, between 10 and 12 µm, and shape.

The present material illustrates that the material belongs to *Nybelinia* subgroup IIIBa of Palm *et al.* (1997), which includes species having an homeoacanthous heteromorphous metabasal armature, a characteristic basal armature and basal hooks smaller than or equal to the metabasal hooks. The species can be easily distinguished from *N. nipponica* Yamaguti, 1952, *N. rougetcampanae* Dollfus, 1960 and *N. yamagutii* Dollfus, 1960 by the lack of bill hooks and the presence of a homeomorphous basal armature. *N. herdmani* can be considered synonymous with *Kotorella pronosoma* (see following), and has a different scolex as well as a different tentacular armature. *Nybelinia southwelli* sp. nov. is similar to *N. beveridgei* Palm, Walter, Schwerdtfeger & Reimer, 1997, the only other species having a homeomorphous basal and heteromorphous metabasal armature. It can be distinguished by a much smaller scolex size, smaller tentacular hooks, 13–14 rows of basal hooks in contrast to 6–7 in *N. beveridgei*, and the absence of a muscular ring around the tentacle sheaths.

It has to be pointed out that though the form and characteristic arrangement of the tentacular armature was the same, *N. southwelli* from the two different elasmobranch species differs slightly in hook sizes along the tentacle. The holotype obtained from *Rhina ancylostoma* had basal hooks with a maximal length of 20, while 3 scolices taken from *Nebrius ferrugineus* had basal hooks with a maximal length of 16. Similarly, the metabasal hooks of the holotype were larger. This observation can be interpreted as a record of morphological variability for *N. southwelli* depending on two different elasmobranch hosts.

Nybelinia perideraeus (Shipley & Hornell, 1906) Dollfus, 1930 (Figs 4–6)

SYNONYMY.

Tetrahynchus perideraeus Shipley & Hornell, 1906

Stenobothrium perideraeum (Shipley & Hornell, 1906) Pintner, 1913

Nybelinia dakari Dollfus, 1960 (new synonymy)

MATERIAL EXAMINED. Co-types VNHM 2109 and 2111; 3 adults from the small intestine of *Glypis gangeticus* (Müller & Henle, 1839) (=*Carcharhinus gangeticus*) (collection of T. Southwell).

DESCRIPTION. The scolex is craspedote (Fig. 4) with a total length (with velum) of 1222, 1092/co-type VNHM 2109 (1352/ co-type VNHM 2111); SW 767, 770 (715), pbo=546, 533 (637), pv=520, 390 (540), pb=408, 461 (429), ppb=59, 16 (69), vel=195, 299 (276), BL=390, 430 (445), BW=103, 114 (115), BR=3.8:1, 3.8:1 (3.9:1), SP=1.3:1.3:1, 1.2:0.8:1 (1.5:1.3:1). A basal tentacular swelling is absent, TW basal=39, 33 (42), TW metabasal=30, 33 (35), TW apical=20, TL=500–570; prebulbar organs and muscular rings around the tentacle sheaths are absent; the retractor muscle inserts in the basal part of the bulbs; TSW=35–40.

The armature is homeoacanthous, heteromorphous, and the hooks of the basal armature are similar to those of the metabasal armature (Figs 5a–b). hsr=6–7. The hooks of the metabasal armature are different in shape and size on bothridial and antibothridial tentacle surfaces (Figs 5a). On the bothridial surface, the tentacular armature consists of strongly recurved, solid hooks with a large base; L=10.5–13.0, B=10.5–11.5. On the antibothridial surface, the hooks are

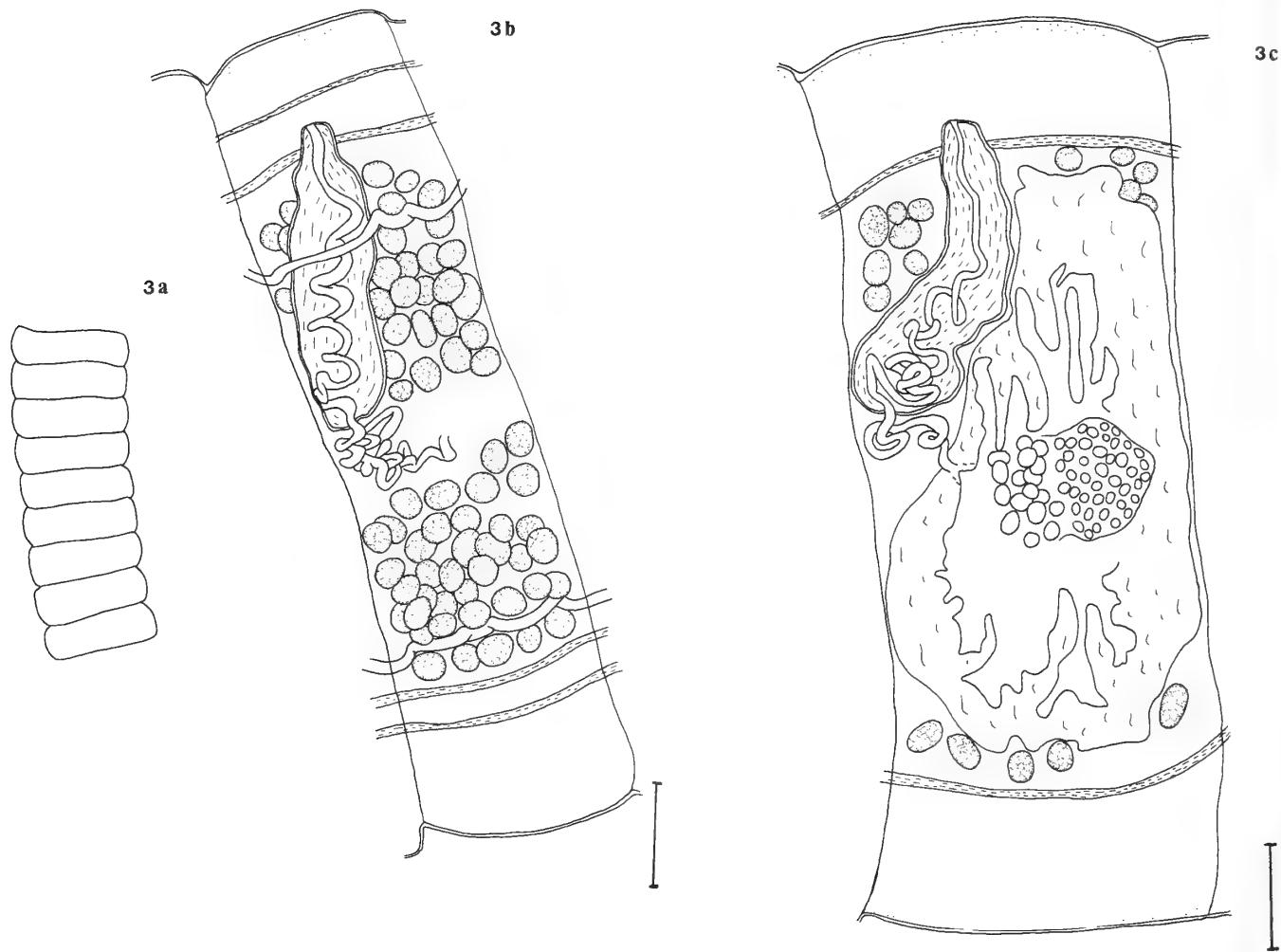


Fig. 3a–c Strobila of *Nybelinia southwelli* sp. nov. a. acraspedote arrangement of the proglottids with characteristic convex margins. b. mature proglottid with the large cirrus sac and oviform testes. c. gravid proglottid. Scale bar b=100 μm and scale bar c=110 μm .

more slender and slightly curved; L=7.5–10.0, B=8–9. The basal armature is heteromorphous (Fig. 5b). The basal hooks are of the same shape and size as those in the metabasal region of the tentacle. External surface hooks, L=10.5–11.5, B=10.5–11.8; internal hooks, L=6.5–8, B=8–9.

The morphology of the mature proglottid of *N. perideraeus* (VNHM 2109) is given as Fig. 6. *N. perideraeus* has a long acraspedote strobila of about 300 proglottids (strobila on 2 slides). While the anterior proglottids are wider than long (520–560 \times 266–300), the final proglottids are longer than wide (559–741 \times 520–530), and continuously increasing in size. The genital atrium is ventrosubmarginal in about the anterior third of the proglottids and alternates irregularly. The cirrus sac is elongate (254 \times 60), directed anteromedially from the genital atrium and the sac is thin-walled. The cirrus is unarmed, coiled within the sac and an internal seminal vesicle was not seen; external seminal vesicle absent. Testes arranged in double layer, number 86–97, ovoid, 33–49 in diameter, encircle the female genital complex, and some testes are present anterior to the cirrus sac. Other details of the female genital complex not seen.

REMARKS.

In the original description of *Tetrarhynchus perideraeus*, Shipley & Hornell (1906) described long worms with a slender scolex bearing long bulbs as well as slender tentacles. The tentacles as well as the tentacular sheaths are short and the tentacular armature consists of oblique rows of very minute hooks of uniform size. However, these characters do not adequately define the species. Dollfus (1930) remarked that without examination of the original material, *N. perideraeus* is not distinguishable from *N. lingualis*. A description of *Stenobothrium perideraeum* by Pintner (1930) did not consider the form and arrangement of the tentacular armature, and thus, was not helpful in solving this taxonomic problem. Southwell (1924, 1929a, 1930) described specimens which he named *N. perideraeus*. However, Pintner (1930) noticed that the material observed by Southwell (1929a, 1930) belonged to a different species.

Dollfus (1942) gave a description of *N. perideraeus*, summarising the information given by Shipley & Hornell (1906) and Pintner (1930), and illustrated the species on basis of material collected from *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) from the Gulf of Suez, Egypt. While remarking that the descriptions of the

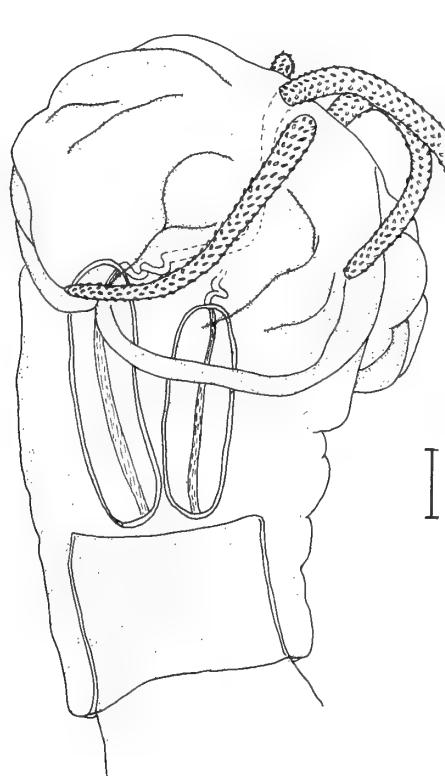


Fig. 4 Scolex of *Nybelinia perideraeus* sp. nov. from *Glypis gangeticus*.
Scale bar=150 µm.

tentacular hooks by Shipley & Hornell (1906) and Pintner (1930) were not unambiguous, he added with his own illustrations given in figs 97–100 a further type of tentacular armature for *N. perideraeus*. He described a characteristic basal armature, where the hook form changes from rose-thorn shaped in the basal part to slender spiniform with sharply recurved tip in the metabasal part. Additionally, the size of the scolex illustrated, 400–500 µm, is much smaller than that given before for *N. perideraeus*. The illustrated specimens from *C. melanoperus* correspond in scolex size and morphology as well as in the detailed described tentacular armature to *N. africana* Dollfus, 1960 (compare Figs 97–100 in Dollfus (1942) with figs 10–19 in Dollfus (1960). Thus, we consider both sets of material to belong to the same species, *N. africana* Dollfus, 1960.

Vijayalakshmi *et al.* (1996) described *N. perideraeus* from *Scoliodon palasorrah* from India with a uniform tentacular armature of minute curved hooks 10 µm long. The co-type material examined in the present study demonstrates that the tentacular armature of *N. perideraeus* is homeoacanthous heteromorphous with rose-thorn shaped tentacular hooks of the same size along the tentacle. Thus, the identity of the material described by Vijayalakshmi *et al.* (1996) still needs to be clarified.

The measurements and figures of the co-type specimen VNHM 2109 as well as the size of the tentacular hooks correspond closely with those of *N. dakari* Dollfus, 1960 from the west African coast and it is therefore considered synonymous with *N. perideraeus*. Thus, *Nybelinia perideraeus* is the only species in subgrouping IIAb of Palm *et al.* (1997), characterized by a homeoacanthous, heteromorphous metabasal armature without a characteristic basal armature and basal tentacular hooks of similar size or bigger than in the metabasal part of the tentacle.

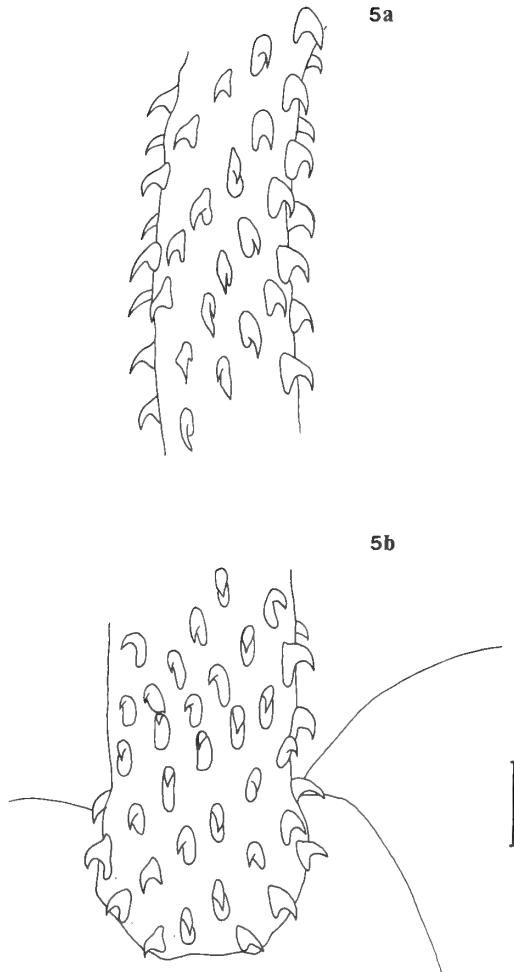


Fig. 5a-b *Nybelinia perideraeus*. a. metabasal tentacular armature, internal surface. b. basal tentacular armature, external surface.
Abbreviation: B=bothridia. Scale bar=20 µm.

Kotorella pronosoma (Stossich, 1901) Euzet & Radujkovic, 1989 (Figs 7–9)

SYNONYMY.

- Rhynchobothrium pronosomum* Stossich, 1901
- Nybelinia pronosomum* (Stossich, 1900) Dollfus, 1930
- Otobothrium pronosomum* (Stossich, 1900) Dollfus, 1942
- Tetrarhynchus herdmani* Shipley & Hornell, 1906 of Southwell (1929a, b 1930)
- Stenobothrium herdmani* (Shipley & Hornell, 1906) Pintner, 1913
- Nybelinia (Nybelinia) herdmani* (Shipley & Hornell, 1906) Dollfus, 1930

MATERIAL EXAMINED. Type VNHM 2095, 1 adult from *Himantura imbricata* (Bloch & Schneider, 1801) (=*Trygon walga*), Sri Lanka (Ceylon) (collection of Shipley & Hornell); VNHM 2097, 1 adult from *Himantura imbricata*, Sri Lanka (collection of Shipley & Hornell).

DESCRIPTION. *Kotorella pronosoma* was described in detail by Euzet & Radujkovic (1989). The scolex measurements of *K. pronosoma* together with the measurements of the type material of

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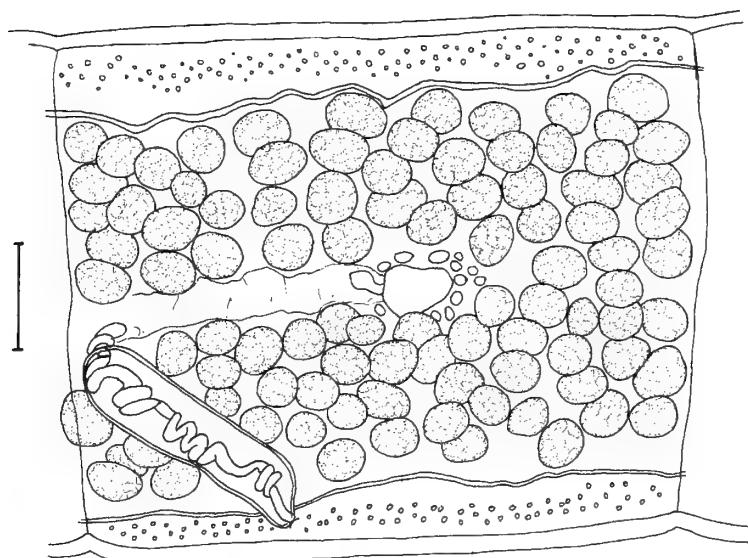


Fig. 6 Mature proglottid of *Nybelinia perideraeus*. Scale bar=100 µm.

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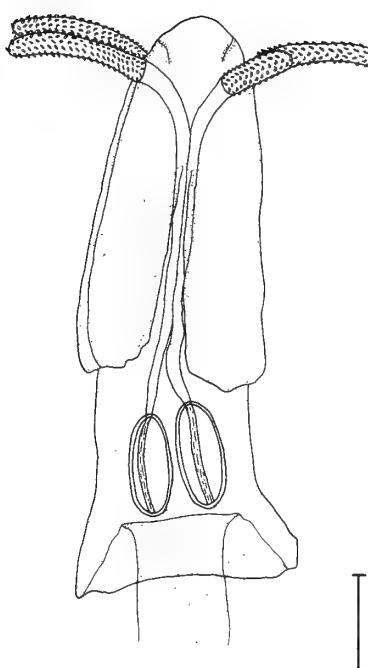


Fig. 7 Scolex of *Kotorella pronosoma* (*Nybelinia herdmani*) from *Himantura imbricata*. Scale bar=150 µm.

N. herdmani are summarised in Table 1. In addition to these data, the following characters were observed: The 4 bothridia of *N. herdmani* (Shipley & Hornell, 1906) have free lateral and posterior margins with a distinct space between the bothridia (Fig. 7). The bothridial margins seem not to be fused with the scolex even apically. Prebulbular organs around the tentacle sheaths are absent and muscular rings are not visible.

The armature of *Kotorella pronosoma* was described by Euzet & Radujkovic (1989) and Campbell & Beveridge (1994). The armature of the type material of *N. herdmani* is homeoacanthous, heteromorphous (Figs 8a–b). The tentacular hooks on the antibothridial tentacle surface increase in size towards the distal part of the tentacle, the hooks on the bothridial tentacular surface are of similar size along the tentacle. The metabasal hooks on the bothridial surface are tightly packed and have a broad, diamond-shaped basal plate ($L=13.5-14.5$, $B=8$). The distance between these hooks appears to be slightly wider towards the apical part of the tentacle. On the antibothridial surface, slender and spiniform hooks without enlarged basal plates increase in size towards the end of the tentacle. The hooks are more widely spaced than on the bothridial surface. Basal hooks: $L=6-8$, $B=2-3$; metabasal hooks: $L=13-14$, $B=3-4$. A basal tentacular swelling is absent. $hsr(\text{basal})=8$, $hsr(\text{metabasal})=6-7$.

The morphology of the mature proglottid of *N. herdmani* is given in Fig. 9. *N. herdmani* has a short acraspedote strobila of about 76 proglottids behind the velum. While the anterior proglottids behind the velum are wider than long ($345-360 \times 20-40$), their length increases in size towards a rectangular shape ($276-310 \times 175-215$). The final proglottids are longer than wide ($715-755 \times 560-610$). The genital atrium is ventrosubmarginal, pre-equatorial and alternates irregularly. The cirrus sac is elongate (242×70), directed medially from the genital atrium and the sac is thin-walled. The cirrus is unarmed, coiled within the sac and an internal seminal vesicle was not seen; external seminal vesicle absent. Testes overlapping but arranged in single layer, number between 35–48. The size of ovoid testes varies depending on number of proglottid (anterior proglottids: 37–47; median proglottids: 53–64; posterior

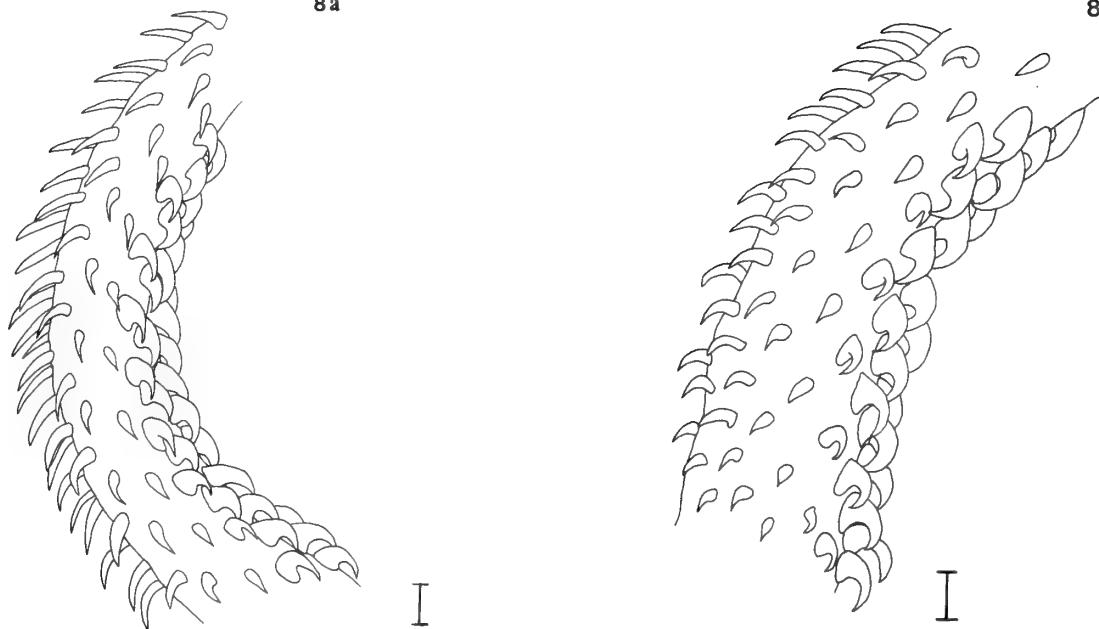


Fig. 8a–b *Kotorella pronosoma* (*Nybelinia herdmani*). a. metabasal tentacular armature, external surface. b. basal tentacular armature, external surface.
Scale bars=10 µm.

proglottids: 71–85 in diameter). Testes encircle the female genital complex (Fig. 9). Female genital complex median.

REMARKS.

In 1906, Shipley & Hornell described *Tetrahynchus herdmani* from the alimentary canal of *Himantura imbricata* and *Rhynchosatys djeddensis* from the Gulf of Mannar (Sri Lanka). However, only a few measurements were given and the tentacular hooks were described as being similar and of the same size (10 µm) along the tentacle. Southwell (1929a) cited Shipley and Hornell (1906) and listed *T. herdmani* with *T. perideraeus* as a species with extremely minute (practically equal in size) hooks arranged in spirals (Southwell, 1929b). Pintner (1930) re-described the type material of *T. herdmani* and reported a homeoacanthous, heteromorphous armature. His description of the tentacles with about 10 small hooks per row, tightly arranged and forming a mosaic on one side, was emended by Dollfus (1942), who reported 14 µm large hooks with a large base. The drawings of Pintner (1930, Figs 67a–b') also give a metabasal hook size between 10–11 µm on the lateral (antibothridial) and 10–14 µm on the medial (bothridial) tentacle surface (7–8 µm of basal antibothridial hooks and 10–14 µm of basal bothridial hooks? / Fig. 67a' and 67b'). Thus, the drawings of the tentacular armature as given by Pintner (1930) correspond to the armature of the type material as described above. Our scolex measurements of the types of *N. herdmani* also correspond to those given by Pintner (1930) and Dollfus (1942) for *N. herdmani* (Table 1).

Euzet & Radujkovic (1989) re-described *Kotorella pronosoma* (Stossich, 1901) from the spiral valve of *Dasyatis pastinaca* L. from the Mediterranean Sea. Though the absolute values of their scolex measurements are about 1/3rd smaller than those given for *Nybelinia herdmani* (Table 1), the scolex and bulb ratios are very similar (see above). The hooks size as given by Euzet & Radujkovic (1989) for *K. pronosoma* is also about 1/3rd smaller (hooks size between 5–8 µm). Campbell & Beveridge (1994, Figs 7.48–7.50) gave additional

figures of the scolex and tentacular armature of *K. pronosoma* with a metabasal/apical hook size of about 10–11 µm (bothridial and antibothridial) and a basal hooks size of about 8–9 µm (bothridial) and 5–6 µm (antibothridial). The arrangement of the tentacular hooks, however, correspond between all specimens of *N. herdmani* and *K. pronosoma* considered above.

The only detailed description of the strobila is given by Euzet & Radujkovic (1989) for *Kotorella pronosoma*. The general morphology of the proglottids (Fig. 2 in Euzet & Radujkovic, 1989), the central female genital complex, the pre-equatorial irregularly alternating cirrus sac and number of testes is corresponding to the type material of *N. herdmani* (Fig. 9). Thus we conclude that both material belongs to the same species, *Kotorella pronosoma* (Stossich, 1901) Euzet & Radujkovic, 1989.

DISCUSSION

With the description of *Nybelinia southwelli* sp. nov. and the synonymy of *N. dakari* with *N. perideraeus* and *N. herdmani* with *Kotorella pronosoma*, the number of adequately described valid species within the genus *Nybelinia* is reduced from 44 to 43. However, the genus remains the most species-rich within the order Trypanorhyncha.

Palm *et al.* (1997) pointed out that the genus *Nybelinia* seems to have many species with a cosmopolitan distribution pattern. In the present study, the two synonymies reported further extend the reported range of distribution for both species. *Nybelinia perideraeus* now can be considered to have a transoceanic distribution. It was originally described from Sri Lanka by Shipley & Hornell (1906), and was re-described as *N. dakari* from the north-west African coast (Dollfus, 1960) and recorded as *N. dakari* from the China Sea by Yang *et al.* (1995). If the specimens labelled *N. perideraeus* in the

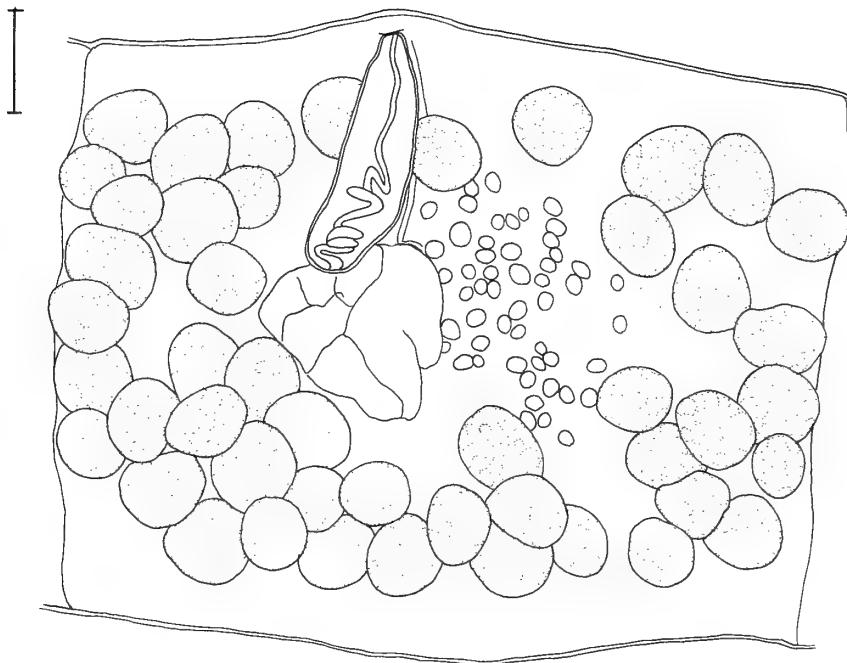


Fig. 9 Mature proglottid of *Kotorella pronosoma* (*Nybelinia herdmani*). Scale bar=100 µm.

Table 1 Scolex measurements (in µm) of *Kotorella pronosoma* (Stossich, 1901) Euzet & Radujkovic, 1989 and *Nybelinia herdmani* (Shipley & Hornell, 1906) (n=number of specimens examined)

species	<i>Kotorella pronosoma</i>		<i>Nybelinia herdmani</i>	
Author / Year	Euzet & Radujkovic (1989)	Shipley & Hornell (1906)	Pintner (1930)	Present study
n	2	¾	—	2
Scolex length:	650	1000	900 (880) ² —1000	980 (900–1060)
Scolex width ¹	—	—	—	374 (297–450)
Pars bothridialis	380	—	600 (570–630)	610 (570–650)
Pars vaginalis	550	—	615 (590–640)	615 (590–640)
Pars bulbosa	110	80–100	155 (150–160)	192 (188–195)
Bulb length	100	Short	160 (140–180)	170 (160–180)
Bulb width	60	—	110 (90–130)	100 (90–110)
Velum	140	—	160 (140–180)	160 (140–180)
Bulb length/bulb width	1,6 : 1	—	1,5 : 1	1,7 : 1
pbo/pv/pb..	3,5 : 5 : 1	—	3,9 : 4,0 : 1	3,2 : 3,2 : 1
Tentacle length	250–275	—	—	308 (260–357)
Tentacle width	12–15	—	—	16–29

¹ Maximum width

² Pintner (1930) in Dollfus (1942)

drawings by Dollfus (1942) are considered to belong to *N. africana*, *N. africana* has now been reported to occur all around Africa, from the Mediterranean, the Gulf of Suez and the north-west and south-east African coasts (Dollfus, 1942, 1960, Palm *et al.*, 1997). Similarly, *Kotorella pronosoma* (*N. herdmani*) is known to occur in the Mediterranean (Euzet & Radujkovic, 1989) and in the Indian Ocean (Shipley & Hornell, 1906). This indicates not only a transoceanic distribution pattern for the tentaculariid trypanorhynch species within the genera *Tentacularia* and *Nybelinia* but also for *Kotorella*. Thus, it seems that the tentaculariid trypanorhynchs *sensu* Palm (1995, 1997) not only demonstrate a remarkable morphological uniformity within the family but also a similar distribution pattern, indicating a

similar life cycle biology. This supports the suppression of the family Kotorellidae Euzet & Radujkovic, 1989, as proposed by Campbell & Beveridge (1994) and Palm (1995, 1997).

The synonymy of *Nybelinia herdmani* with *Kotorella pronosoma* demonstrates the high similarity between species belonging to these two tentaculariid genera. However, in *K. pronosoma*, the basal hooks with a diamond shaped basal plate also demonstrate a similarity to the basal hooks of *Tentacularia coryphaenae* Bosc, 1797 (see Figs 2–4 in Palm, 1995). Additionally, a wide space between the elongated bothridia appears to be characteristic only for these two genera, which is in contrast to more triangular and more tightly spaced bothridia within the genus *Nybelinia*. These differences still

justify the genus *Kotorella* Euzet & Radujkovic, 1989 within the Tentaculariidae Poche, 1926. However, the gross morphological characters such as scolex form, proportions and form of the bulbs indicate a close phylogenetic relationship between *Kotorella* and *Nybelinia*, as proposed by Campbell & Beveridge (1994) and Palm (1995, 1997). Interestingly, a cladistic analysis of the genera within the Trypanorhyncha failed to assign the genus *Kotorella* to the same clade as the other tentaculariid genera (Beveridge *et al.*, 1999).

The scolex measurements for *Nybelinia southwelli* sp. nov. appear to be variable. Although having a similar scolex size to the holotype, the tentacular hooks of the paratype were distinctly smaller. It appears that measurements of armature within a species can show variability as do other scolex measurements, e.g. scolex length (*N. nipponica*: 1.35–2.9; *N. karachii*: 1.25–2.5 (Yamaguti, 1952, Kurshid & Bilquees, 1988)), scolex width (*N. beveridgei*: 2.1–3.1; *N. thyrsites*: 0.66–1.06 (Palm *et al.*, 1997, Beveridge & Campbell, 1996)) and bulb length (*N. nipponica*: 310–550 (Yamaguti, 1952)). The synonymy of *Nybelinia herdmani* with *Kotorella pronosoma* gives a further example on scolex variability within tentaculariid trypanorhynchs. The absolute values of scolex measurements as well as hook sizes varied about 1/3rd of total value between the different specimens. *Kotorella pronosoma* as described by Euzet & Radujkovic (1989) can be considered as smaller specimens than the material examined by us, which is reflected in both, smaller scolex measurements and smaller hooks. This observation generally questions the usage of minor absolute values in scolex and hook measurements as main species distinguishing characters within tentaculariid cestodes. A similar variability in the scolex morphology of trypanorhynch plerocerci has been demonstrated for *Otobothrium penetrans* by Palm *et al.* (1993). Whether such differences are generally due to different host species or a different age of the postlarvae, plerocerci or adults compared cannot be decided at present.

This variability within trypanorhynch cestodes has resulted in the description of several invalid species, especially within the genus *Nybelinia*, as proposed by Palm *et al.* (1997). However, the subgrouping of *Nybelinia* species based on characters of the tentacular armature appears to be a useful tool for further taxonomic studies within the genus (see Palm *et al.*, 1997). In the present study, all species within the subgroupings IIAb and IIBa are clearly defined. Further studies are needed to clarify the validity of species within the other 6 groupings, leading to a complete revision of the genus *Nybelinia*.

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***Nybelinia* Poche, 1926, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov. (Cestoda, Trypanorhyncha) in the collections of The Natural History Museum, London**

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SYNOPSIS. With a total of 43 adequately described species, the cosmopolitan genus *Nybelinia* is the most species-rich genus within the order Trypanorhyncha. As an initial part of a revision of the genus, the present study was carried out to examine unidentified and identified *Nybelinia* specimens deposited at The Natural History Museum London. A total of 17 different species was found, four new species are described and 2 new genera, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov., are erected: *Nybelinia aequidentata* (Shipley & Hornell, 1906); *N. africana* Dollfus, 1960; *N. jayapaulazariahi* Reimer, 1980; *N. lingualis* (Cuvier, 1817); *N. riseri* Dollfus, 1960; *N. sakanariae* sp. nov.; *N. schmidti* sp. nov.; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) comb. nov.; *Nybelinia* sp.; *Heteronybelinia elongata* (Shah & Bilgees, 1979) comb. nov.; *H. estigmrena* (Dollfus, 1960) comb. nov.; *H. heteromorphi* sp. nov.; *H. minima* sp. nov.; *H. robusta* (Linton, 1890) comb. nov.; *H. yamagutii* (Dollfus, 1960) comb. nov.; *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) comb. nov. and *M. southwelli* (Palm & Walter, 1999) comb. nov.. *Tentacularia scoliodoni* is transferred to the genus *Nybelinia*. Nine new locality and 15 new host records were established. The adults of *Heteronybelinia estigmrena* and *H. yamagutii* are reported for the first time. It is proposed that the morphological variation within the different species is much higher than considered in the recent literature. Many species within the genus have a world-wide distribution pattern and a low host specificity, both in their fish second intermediate/paratenic hosts and in their final hosts.

INTRODUCTION

Trypanorhynchs are cosmopolitan marine cestodes and mature in the stomach or the spiral valve of marine elasmobranchs, while their postlarvae are parasitic in teleosts and invertebrates, with the first intermediate hosts being crustaceans (Palm, 1997a, Sakanari & Moser, 1989). Within the order Trypanorhyncha, the genus *Nybelinia* Poche, 1926 is particularly difficult to study. Palm *et al.* (1997) listed 43 adequately described species while leaving 4 as species of uncertain status. Jones & Beveridge (1998) added a further species, *N. queenslandensis*, and Palm & Walter (1999) described *N. southwelli*, and synonymised *Nybelinia dakari* Dollfus, 1960 and *N. herdmani* (Shipley & Hornell, 1906) with *N. perideraeus* (Shipley & Hornell, 1906) and *Kotorella pronosoma* (Stossich, 1901) respectively. Thus, with a total of 43 adequately described species, the genus *Nybelinia* is the most species-rich genus within the order Trypanorhyncha.

In contrast our knowledge of their biology is poor. The first intermediate hosts are unknown and the occurrence of postlarvae in marine plankton (Dollfus, 1974) is enigmatic. Postlarvae of these robust worms are found in unusual sites such as the human palatine tonsil (Kikuchi *et al.*, 1981) as well as in anadromous *Lampetra japonica*, 1000–3000 km away from the sea in the Amur river (Shulman, 1957). Additionally, members of the genus *Nybelinia* infest the fish flesh (Oshmarin *et al.*, 1961, Palm, 1997b), and parasitic infestation of the musculature of commercially important fish species causes heavy losses to the fish processing industry (Arthur *et al.*, 1982, Deardorff *et al.*, 1984).

One of the biggest problems for taxonomic work within the genus

Nybelinia, apart from incomplete original descriptions, remains the lack of information on material deposited in museum collections. The genus has not been revised since 1942, and due to the morphological similarity of several species, many *Nybelinia* specimens found have not been identified to species level, and consequently have been deposited as *Nybelinia* sp. Additionally, several species descriptions are based on single specimens.

The present study was carried out to examine unidentified species of *Nybelinia* deposited at The Natural History Museum, London. Measurements and drawings of most specimens are given as verification of the identifications made. Beside the establishment of new host and locality records, species identifications provide further insight into the zoogeographical distribution. The comparison of the scolex measurements with those from original descriptions allows comments to be made on the level of intraspecific morphological variation of some *Nybelinia* species, data which are necessary for further taxonomic studies within the genus. The description of adult specimens allows comparative investigations on strobilar morphology within the genus.

MATERIAL AND METHODS

Standard measurements and drawings of the scoleces of *Nybelinia* specimens deposited in the Parasitic Worms Division, The Natural History Museum, London (BMNH), were made using a Leitz Wetzel Dialux 20 microscope with an ocular micrometer. Special attention was given to unidentified specimens deposited simply as *Nybelinia* sp., while other deposited and identified material was also examined.

ined. As additional material, slides from the Natural History Museum, Vienna (NHMV No. 2111) and from the U.S. National Parasite Collection, Beltsville (USNPC No. 7727 (M130-6)) were borrowed. Similarly, deposited *Nybelinia* species were studied in the Muséum National d'Histoire Naturelle, Paris (MNHN Paris), for comparison.

The following measurements were made: Scolex length (SL), scolex width at level of pars bothridialis (SW), pars bothridialis (pbo), pars vaginalis (pv), pars bulbosa (pb), pars postbulbosa (ppb), velum (vel), appendix (app), bulb length (BL), bulb width (BW), bulb ratio (BR), proportions of pbo/pv/pb (SP), tentacle width (TW), and tentacle sheath width (TSW). If possible, the tentacle length was estimated. Additionally, the tentacular armature was described as follows: armature homeomorphous or heteromorphous, hooks per half spiral row (hsr), total hook length (L) and the total length of the base of the hooks (B). The abbreviation nm (not measured) indicates that no measurement was taken.

All measurements are given in micrometers unless otherwise indicated. Specimens belonging to the same species from different hosts or localities were measured in the same order as the specimens are listed under Material examined. If more than two measurements were taken, the mean is given with the range in parentheses, unless otherwise indicated. Illustrations are provided if useful for future identification of the species; otherwise the reader is referred to illustrations of other authors. The classification follows that of Palm (1995, 1997a) and the orientation of the tentacular surfaces follows that of Campbell & Beveridge (1994).

RESULTS

A total of 17 species was identified, and 4 new species are described. Nine new locality and 15 new host records were established. The information on the single specimens measured with comments on their taxonomy and distribution are given below.

Superfamily TENTACULARIOIDEA Poche, 1926

Family TENTACULARIIDAE Poche, 1926

Genus *NYBELINIA* Poche, 1926

1. *Nybelinia aequidentata* (Shipley & Hornell, 1906) (Figs 1–2)

MATERIAL EXAMINED. BMNH 1992.7.1.193–196, A. Roy leg., 1 postlarva from *Lepturacanthus savala*, Sugar Island, Bay of Bengal.

DESCRIPTION. The type material of *N. aequidentata*, which is deposited at the Natural History Museum, Vienna, was re-described by Pintner (1927). The scolex and tentacular armature of the present specimen is given in Figs 1–2. Measurements: SL=3400; SW=1700; pbo=1510; pv=1890; pb=813; ppb=57; vel=530; app=585; BL=780 (756–813); BW=237 (227–265); BR=3.3:1; SP=1.9:2.3:1. TW metabasal=54–58, TW apical=46–51. A basal tentacular swelling is absent. The tentacle sheaths are straight; TSW=33–38. Prebulbar organs are absent, muscular rings around the basal part of the tentacle sheaths are present. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, homeomorphous, and a characteristic basal armature is absent. The massive hooks of the metabasal armature are similar in shape (Fig. 2), diminishing in size from the 6th row towards the basal part of the tentacle. The size of the hooks also diminish slightly towards the apical end of the tentacles. The

hook size in the metabasal armature was L=33–38, B=13–17; hsr=8.

REMARKS. The present specimen is similar to the type material, having a large scolex and pbo and slender tentacular hooks with a long shaft and a rounded base. The tentacular hooks of the type specimen are similarly shaped along the tentacle and diminish in size towards the tip and at the base (compare with Pintner 1927, p. 562). Additionally, both specimens were found in the same region, off the Indian coast. However, the present specimen also shows some differences to those described by Shipley & Hornell (1906) and Pintner (1927). The scolex measurements of the type (4500–5000, SW=2000) as well as the hook sizes (L=up to 48) are larger. Similarly, the scolex proportions of the two specimens differ (type: BR=4.3:1 and SP=1:1.7:1). In both cases, the descriptions are based on a single specimen only, and no data on the morphological variability within *N. aequidentata* are available.

The present specimen belongs to subgroup IAa of Palm *et al.* (1997) and due to the characteristically shaped slender hooks with a rounded base, slender shaft and strongly re-curved tip, it has similarities with *N. edwinlintoni* and *N. goreensis*. *N. edwinlintoni* is smaller, has a different bulb ratio (2.5:1) and scolex proportion (2.4:1.6:1) as well as a larger TW, TSW and smaller (L=18–20, B=10) hooks (Dollfus, 1960). *N. goreensis* is also smaller (SL=1235–1325), has a slightly different bulb proportion (2.5–3:1), a larger TW, TSW and smaller hooks. In addition, Dollfus (1960) remarked on the uniformity of the hooks. Two species with a similar tentacular armature, *N. anantaramanorum* and *N. syngenes*, were placed in subgroup IAb by Palm *et al.*, 1997, with hooks of similar size in the basal and metabasal part of the tentacles. *N. anantaramanorum* from the Gulf of Bengal differs in having smaller hooks and a smaller scolex (Reimer, 1980). However, there is a close relationship between *N. aequidentata* and *N. anantaramanorum*. *N. syngenes* resembles the present specimen in having similar tentacular hooks. However, it clearly differs by having a distinctly smaller scolex and larger hooks (L=68; Pintner, 1929, Dollfus, 1942). Thus, the present specimen is identified as *N. aequidentata*, and represents a new host record. However, the similarities between these species have to be kept in mind.

2. *Nybelinia africana* Dollfus, 1960

(Fig. 3)

MATERIAL EXAMINED. BMNH 1982.4.6.37–45, R. van der Elst leg., 11.05.1984, 1 adult from the lower gut/upper intestine of *Carcharhinus obscurus*, South Africa; BMNH 1985.11.8.63–64, R. van der Elst leg., 11.5.1984, 1 adult from *Carcharhinus leucas*, Richards Bay, South Africa. Other material: BMNH 1982.4.6.18–22, R. Bray leg., from the lower stomach of *Carcharhinus obscurus*, Durban, South Africa; BMNH 1985.11.8.53–54, R. van der Elst leg., 2.4.81, from the stomach of *Carcharhinus leucas*; BMNH 1985.11.8.55–56, R. Bray leg., from the stomach of *Mustelus canis* (=*M. canis* or *M. queketti*), stomach, Durban, Natal.

DESCRIPTION. *Nybelinia africana* was described in detail by Dollfus (1960, see figures 9–19) and Palm *et al.* (1997). Measurements: SL=536, 440; SW=420, 485; pbo=327, 337; pv=205, 122; pb=178, 150; vel=210, 164; BL=174 (168–178), 133 (120–150); BW=73 (70–75), 70 (60–78); BR=2.4:1, 1.9:1, SP=1.8:1.1:1, 2.2:0.8:1; Short tentacles, about 200 long, with TW basal=28, 27; TW metabasal 23, 24; The tentacle sheaths are sinuous or spirally coiled, TSW=18–23, 17–20. The characteristic tentacular armature is homeomorphous with a basal armature of about 6 rows with rose-thorn-shaped hooks. The metabasal armature consists of slender hooks with a strongly re-curved tip (L=13.5–15.2, 12.5–14.8; B=5.6–7.2, 4.0–5.5). The tentacular hooks of the basal armature were

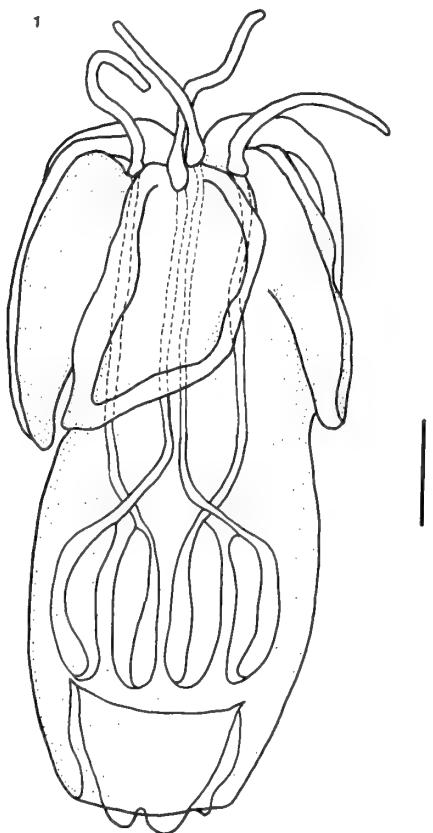


Fig. 1 *Nybelinia aequidentata* isolated from *Lepturacanthus savala*.
Scolex. Scale bar=500 µm.

rose-thorn shaped ($L=9.6\text{--}12.0$, $8.8\text{--}12.0$; $B=7.2\text{--}8.8$, $7.2\text{--}8.8$); $hsr=7\text{--}8$.

The strobila is acraspedote, with about 240 segments, last proglottid with rounded proximal end. The first 70 proglottids are very short ($10\text{--}50$ long \times $370\text{--}530$ wide), the next enlarge in size towards $400\text{--}500 \times 940\text{--}1030$. The last 20 proglottids are a bit wider than long $1050\text{--}1200 \times 1250\text{--}1450$. In mature proglottids (Fig. 3), genital atrium ventro-submarginal, in anterior half of the segment; genital pores alternate irregularly. Cirrus sac elongate and slender, 80×450 in size, directed anteromedially, sac thin-walled; cirrus unarmed and coiled within sac, internal and external seminal vesicle not seen; vas deferens coils medially to mid-line, then posteriorly towards genital complex. Testes of different shape, often ovoid, $70\text{--}95$ in diameter ($55\text{--}70$ in proglottids $71\text{--}160$), arranged in a single layer; testes number $80\text{--}90$ per proglottis, encircle female genital complex and occupy entire medulla except for region of female genital complex and anterior of it. Ovary centrally, follicular, x-shaped with 2 major branches, each 95×160 . Uterine ducts coiled before they enter the sacciform uterus. Vitelline follicles $25\text{--}35$ in diameter.

REMARKS. Dollfus (1960) described larvae of *N. africana* from the body cavity of *Galeoides polydactylus*, *Mullus barbatus*, *Pagellus* sp., *Serranus cabrilla*, and *Trigla* sp.. The 3 scoleces measured by Dollfus were variable in size, ranging for example between $750\text{--}1100$ (SL), $397\text{--}540$ (pbo) and $19\text{--}35$ (TW). The BR and SP were between $2.6:1\text{--}3.4:1$ and $2.1:0.9:1\text{--}2.3:1.4:1$ respectively and the hook size in the metabasal armature was between $14\text{--}17$. The

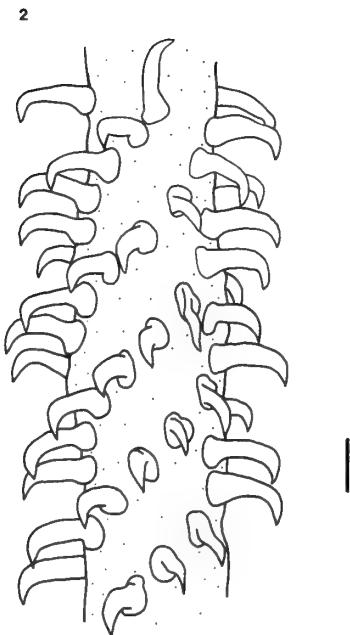


Fig. 2 *N. aequidentata*. Homeomorphous metabasal armature. Scale bar=25 µm.

measurements for the present specimens were smaller and only the SP of the specimen from *Carcharhinus leucas* directly corresponds to specimen in tube 465 described by Dollfus (1960). However, the similar form and size of the basal and metabasal hooks together with a similar TW lead to the identification proposed. Palm *et al.* (1997) reported specimens of *N. africana* from the Mozambique coast which were larger in scolex and hook sizes than the above material. However, the form of the hooks along the tentacle as well as the BR, SP and TW were similar to those described by Dollfus (1960). Thus, it seems that *N. africana* has a variable scolex size, and, depending on this, a different hook size. However, the characteristic hook forms along the tentacle remain the same. Palm & Walter (1999) recognised adults of *N. africana* from *Carcharhinus melanopterus* from the Gulf of Suez, Egypt (named as *N. perideraeus* in Dollfus, 1942) on bases of the scolex size and the tentacular armature, and the present description of adult *N. africana* supports this synonymy. The strobila characters of the present specimens correspond with that of Dollfus's description in a similar size and shape of the first ($10\text{--}50 \times 370\text{--}530$ vs 11×290) and last ($1050\text{--}1200 \times 1250\text{--}1450$, a bit wider than long vs 1100×900 , a bit longer than wide) proglottids, the follicular ovary, and similar sized vitellaria ($25\text{--}35$ vs $26\text{--}31$). The present study records specimens from two further carcharhinid shark species and from *Mustelus canis* from South Africa. They represent new host and locality records, which indicates a circum-African distribution and a low host specificity of adult *N. africana*, as was earlier proposed for the postlarvae by Palm *et al.* (1997).

3

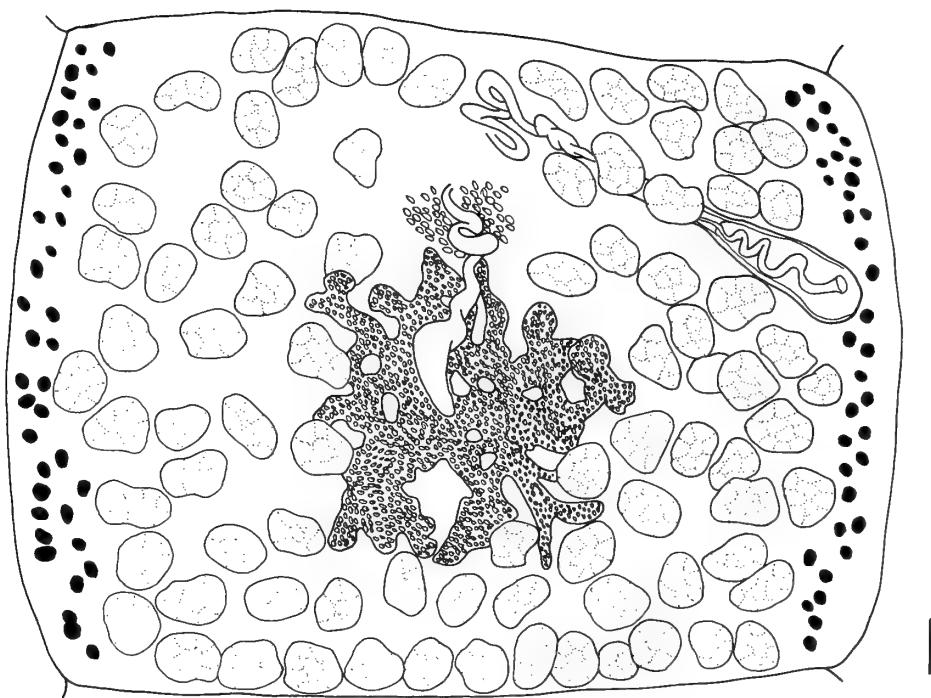


Fig. 3 *N. africana*. Mature segment. Scale bar=60 µm.

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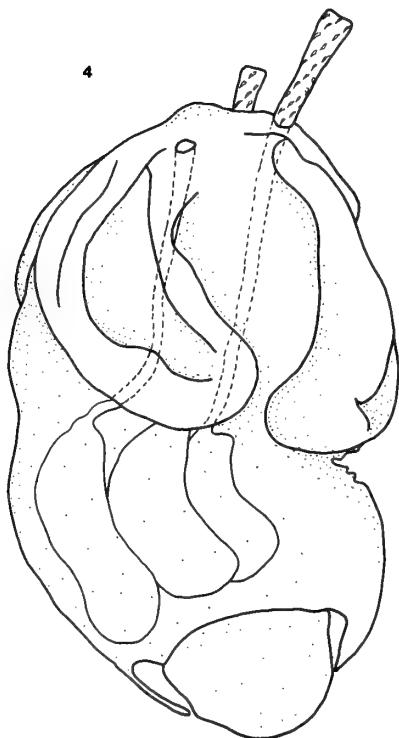


Fig. 4 *Nybelinia jayapaulazariahi* from *Harpodon nehereus*. Scolex.
Scale bar=50µm.

5

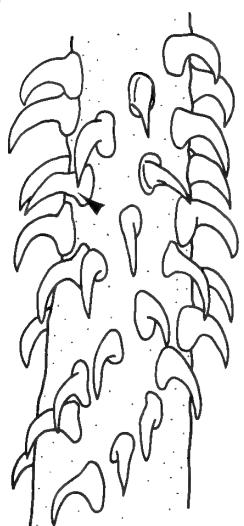


Fig. 5 *N. jayapaulazariahi*. Homeomorphous metabasal armature with slender hooks, metabasal hook as given in Reimer (1980), figure 4 (arrow). Scale bar=10 µm.

3. *Nybelinia jayapaulazariahi* Reimer, 1980 (Figs 4–5)

MATERIAL EXAMINED. BMNH 1980.12.2.1, A. Roy leg., 14.9.79, 1 postlarva from *Harpodon nehereus*, Houghly estuary, India (Figs 4–5).

DESCRIPTION. Measurements: SL=530; SW=326; pbo=298; pv=285; pb=165; app=114; vel=96; BL=157 (150–165); BW=54; BR=2.9:1; SP=1.8:1.7:1; TW=16–18.5; TSW=12.5–15.5; a basal tentacle swelling is absent; the tentacle sheaths are straight; Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous, and a characteristic basal armature is absent. The size of the slender, regularly curved hooks increases slightly towards the metabasal part of the tentacle; L=9.6–11.2; B=5.6–7.2 (metabasal) and L=5.6–7.2; B=5.6–7.2 (basal); hsr=6.

REMARKS. The present specimen from *Harpodon nehereus* corresponds closely with that of the original description by Reimer (1980) from *Cynoglossus* sp.. Beside a similar scolex form (Fig. 7 in Reimer, 1980) and similar scolex and bulb ratios (SP 1.9:–1 and BR 3:1), the hook size is identical and the hook form (as given in Reimer, 1980, Fig. 8) resembles that given in Fig. 5 (see arrow). The hook form with its slender, regularly curved shaft is distinct from the robust rose-thorn shaped hooks of many other *Nybelinia* species. The values of the TW extracted from Fig. 7 of Reimer are slightly higher (ca. 20–25 µm) than those of the present specimen. Both specimens were found in the same part of the Indian Ocean, Houghly estuary, India, and the Bay of Bengal, India. *Harpodon nehereus* represents a new host for *Nybelinia jayapaulazariahi*.

4. *Nybelinia lingualis* (Cuvier, 1817) (Figs 6–9)

MATERIAL EXAMINED. BMNH 1987.3.2.19, R. Bray leg., 1 postlarva from the gut of *Torquigener pleurogramma*, Adelaide, South Australia; BMNH 1987.4.23.11–12, R. Bray leg., 03.12.1986, 2 postlarvae from the branchial chamber of *Arnoglossus imperialis*, Cirolana 76–78 m, 49°50'5"N, 3°44'3"W; BMNH 1987.4.23.18–32, R. Bray leg., 03.12.1996, 1 postlarva from the intestinal wall of *Pagusa lascaris*, Cirolana, English Channel, 49°50'5"N, 3°44'3"W, 76–78 m.

DESCRIPTION. *Nybelinia lingualis* was described in detail by Dollfus (1942). The scolex of the specimen from *T. pleurogramma* is shown in Fig. 6. Measurements: SL=1606, 1720, 1700, 2040; SW=718, 982, 907, 1172; pbo=700, 1096, 1096, 1172; pv=642, 907, 907, 1171; pb=397, 321, 298, 341; ppb=75, 0, 0, 10; app=490, 510, 491, nm; BL=365 (326–397), 313 (303–322), 292 (289–294), 341; BW=138 (130–140), 128 (117–140), 114 (112–117), nm; BR=2.6:1, 2.4:1, 2.6:1, nm; SP=1.8:1.6:1, 3.4:2.8:1, 3.7:3:1, 3.4:3.4:1. The tentacles are long and slender and diminish in diameter towards the tip; TW basal=39, 42, 46, 46, TW metabasal=32, 33, 33, 38; TW distal=24, nm, nm, nm. A basal tentacular swelling is not present. The tentacle sheaths are coiled in 1 to 2 spirals near the bulbs; TSW=36, 46, 42, 40. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, homeomorphous, and a characteristic basal armature is present (Figs 7–9). The tentacular hook form changes towards the apical part of the tentacle from compact, rounded rose-thorn (Fig. 7), lacking an posterior extension of the basal plate, to more slender rose-thorn shaped hooks (Figs 8–9). The hooks in the basal part of the tentacle are smaller (L=11.0–13.0,

11.6–13.6, 11.6–13.6, 11.6–13.6; B=9.3–11.2, 7.2–9.6, 7.2–9.6, 7.2–9.6) than in the metabasal armature (L=14.5–16.7, 16.0–18.4, 16.0–18.4, 16.0–18.4; B=9.3–13.0, 12.0–13.5, 12.0–13.5, 12.0–13.5). The number of hooks per half spiral diminish towards the apical part of the tentacle; hsr=6–7 (basal), hsr=5–6 (apical).

REMARKS. The present specimens correspond with those described by Dollfus (1942). Although the scolex measurements as well as hook sizes are smaller than those given by Dollfus (1942), the scolex form as well as the form and arrangement of the tentacular hooks correspond with drawings of *N. lingualis* found in *Sepia filliouxi*, *S. officinalis* and *Mullus barbatus* (see Dollfus, 1942, Figs 88–91). According to Dollfus (1942), the bulbs are typically short (about 300–400 µm long), with a BR of about 2.2–2.5:1. Additionally, Dollfus (1942) demonstrated a high degree of morphological variability within the species with a scolex size between 1.2–3.2 mm. As with *Tentacularia coryphaenae*, *Nybelinia lingualis* has a wide zoogeographical distribution and a low host specificity. The present findings with the exception of specimens in *Pagusa lascaris* are new host records and extend the known range of distribution for the species to Australian waters. Palm (1995) examined specimens of the same species (BMNH 1987.4.23.18–32 from *P. lascaris*) and tentatively identified them as *N. lingualis*. The present finding confirms this identification. Thus, the surface morphology of *Nybelinia lingualis* with filiform microtriches on the distal bothridial surface and hook-like microtriches on the bothridial borders corresponds to those as described for *Tentacularia coryphaenae*, *N. alloiotica*, *N. edwinlintoni*, *N. queenslandensis* and *N. c.f. senegalensis* (Palm, 1995, Jones & Beveridge, 1998).

5. *Nybelinia riseri* Dollfus, 1960

(Figs 10–11)

MATERIAL EXAMINED. BMNH 1985.11.8.65, G. Ross leg., 30.11.1979, 3 postlarvae from *Trachyurus felicipes* (Figs 10–11), stomach wall, East Cape, South Africa.

DESCRIPTION. Measurements: SL=1455 (1380–1587); SW (pbo)=580 (510–680); SW (pv)=400 (300–454); pbo=630 (585–662); pv=636 (567–700); pb=294 (280–303); ppb=204 (151–233); app=331 (312–360); BL=284 (270–303); BW=100 (84–117); BR=2.8:1 (2.7:1–3.2:1); SP=2.1:2.2:1. The tentacles are not completely evaginated, a basal tentacle swelling is absent. TW=51–56. The tentacle sheaths are straight and the TSW without invaginated tentacles is nearly half as small (TSW=23–28) than with invaginated tentacles (TSW=42–46). Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous, and consists of compact rose-thorn-shaped tentacular hooks (upper basal armature, L=14–19; B=12–15). The hooks are in tight spirals (Fig. 11) and the hooks diminish in size towards the basal part of the tentacles (L=12–14; B=9–12); hsr=6–7.

REMARKS. Only two species, *N. riseri* and *N. lingualis*, have been described as having a similar champion-shaped scolex form as well as a homeoacanthous, homeomorphous tentacular armature such as described for the present specimens. *N. riseri* is characterised by the champion-shaped scolex (see Dollfus, 1960), however, the hooks in the basal part of the tentacle (L=11–12, B=11–12) are smaller than observed for the present specimens. *N. lingualis* corresponds with a similar basal armature (see above) and scolex proportions as described for specimens of *N. lingualis* taken from *Trachyurus felicipes* (see Dollfus, 1942). However, the general scolex form with the small banana-shaped bulbs of *Nybelinia lingualis* (see Dollfus, 1942) clearly differs to the present specimens. Thus, they are

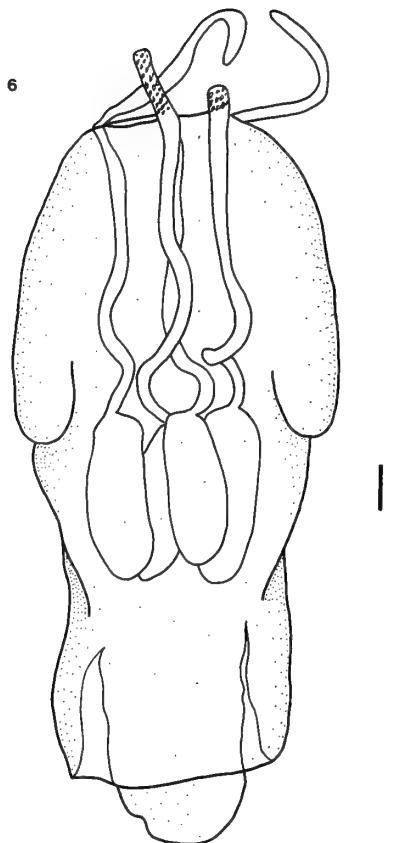


Fig. 6 *Nybelinia lingualis* from *Torquigener pleurogramma*. Scolex.

Scale bar=100 µm.

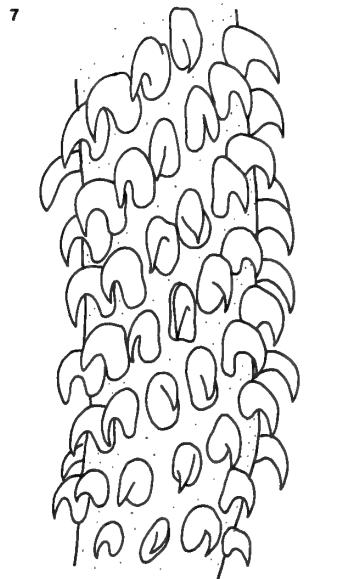


Fig. 7 *N. lingualis* from *T. pleurogramma*. Homeomorphous basal armature consisting of rounded hooks without anterior extension of the basal plate. Scale bar=10 µm.

identified as belonging to *Nybelinia riseri* on basis of the characteristic scolex form. It has to be kept in mind that the tentacles of the present specimens were not completely evaginated. The present finding represents a new host and locality record.

6. *Nybelinia akanariae* sp. nov. (Figs 12–13)

MATERIAL EXAMINED. Holotype and paratype, BMNH 1976.1.7.9, Hecht leg., 2 postlarvae from the stomach of *Xiphurus capensis*, South Africa. Additional material: BMNH 1976.1.7.7–8, Hecht leg., 1 postlarva from the testes of *Trachurus trachurus*, Algoa Bay, South Africa.

DESCRIPTION (Fig. 12). Measurements: SL=1512, 1507; SW=775, 747; pbo=700, 700; pv=680, 647; pb=397, 386; ppb=94, 100; vel=360, 335; app=360, 335; BL=387, 335; BW=116, 113; BR=3.3:1, 3:1; SP=1.8:1.7:1, 1.8:1.7:1. A basal tentacle swelling is absent. TW=51–56. The tentacle sheaths are short, little coiled with a TSW=51–56. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, homeomorphous, and consists of compact rose-thorn-shaped tentacular hooks (Fig. 13); upper basal and metabasal armature, L=16–22; B=13.5–17.0. Characteristic basal hooks are absent. However, the hooks diminish in size towards the basal part of the tentacles (L=12–14; B=11–13); hsr=6–7.

ADDITIONAL MATERIAL. SL=3270; SW=1020; pbo=1134; pv=1172; pb=605; ppb=567; vel=756; app=740; BL=580; BW=147; BR=3.9:1; SP=2:2:1. The tentacles are short and a basal tentacle swelling is absent. TW=56–61. The tentacle sheaths are straight, prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs. Metabasal armature, L=21–23; B=15–17. A characteristic basal armature is absent, the hooks diminish in size towards the basal part of the tentacles (L=11–13; B=11–13); hsr=7.

REMARKS. The present specimens correspond with *Nybelinia strongyla* in having a similar scolex, SP, BR, TW and a similar hook size. However, the scolex size is smaller than indicated by Dollfus (1960) and the type material deposited at the MNHN Paris revealed a different hook shape. The material also resembles *N. riseri* as described by Dollfus (1960) with corresponding values of SL, BL, BW, BR, ppb and a similar basal hook size. The hook form of *N. riseri* appears massive with a broad base, and hooks are tightly packed along the tentacle. However, the hooks of the armature of *N. riseri* of about 11–12 µm are distinctly smaller than in the present specimens, and the characteristic scolex form of *N. riseri* (see above) was not present. The specimens also have some similarities with *Nybelinia queenslandensis* Jones & Beveridge, 1998 with a similar hook form. However, the specimens clearly differ in having the hooks more tightly spaced and different values for SL, TW, BR and SP. Thus, the present specimens represent a new species, *Nybelinia akanariae* sp. nov. Interestingly, the additional material obtained from another host had a much larger scolex than observed

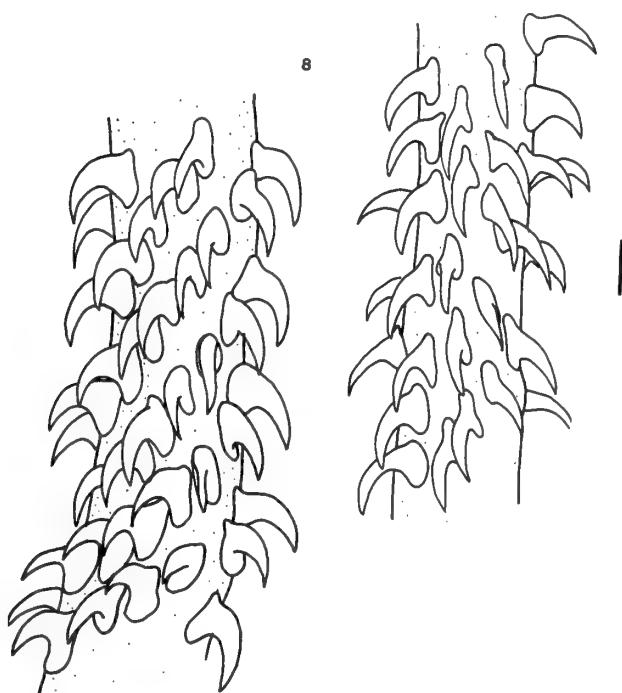


Fig. 8 *N. lingualis* from *T. pleurogramma*. Homeomorphous metabasal armature. Scale bar=10 µm.

Fig. 9 *N. lingualis* from *T. pleurogramma*. Homeomorphous apical armature. Scale bar=10 µm.

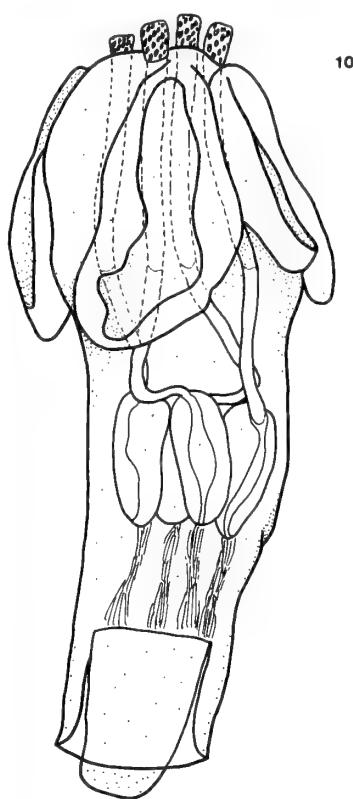


Fig. 10 *Nybelinia riseri*. Scolex from *Trachyurus felipes*. Scale bar=100 µm.

for the type material but the same kind of tentacular armature. The size should be considered as a case of intraspecific morphological variability within the species.

ETYMOLOGY. The new species is named after J.A. Sakanari, in honour to her work on the life cycle of trypanorhynch cestodes.

7. *Nybelinia schmidti* sp. nov. (Figs 14–15)

MATERIAL EXAMINED. Holotype BMNH 1982.12.3.1, G. Ross leg., 23.07.1978, 1 adult from the stomach of *Isurus glaucus*, Algoa Bay, South Africa.

DESCRIPTION (Figs 14–15). Measurements: SL=1172; SW=832; pbo=794; pv=473; pb=289; ppb= 46; vel=373; BL=289; BW=104 (94–117); BR=2.8:1; SP=2.7:2.6:1. The tentacles are long and slender; TW=18.4–23.5; and a basal swelling is absent. The tentacle sheaths are spirally coiled; TSW=46–51. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous, and a characteristic basal armature is absent. The massive and rose-thorn shaped hooks increase in size towards the metabasal part of the tentacle, L=13.5–15.0; B=11.7–13.3 (metabasal) and L=9.0–10.3; B=8.3–9.0 (basal); the hooks in the metabasal part of the tentacle are slightly more slender than in the basal part; hsr=5–6.

The strobilar is acraspedote, with about 240 very large segments, wider than long. The proglottids in the anterior part of strobila are 140–155 long × 1400–1540 wide, the final proglottids enlarge in size towards 450–560 × 2800–3080. In mature proglottids, genital

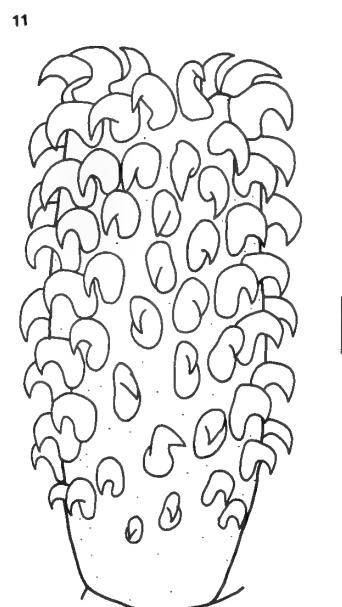


Fig. 11 *N. riseri*. Homeomorphous basal armature consisting of rounded hooks without anterior extension of the basal plate. Scale bar=15 µm.

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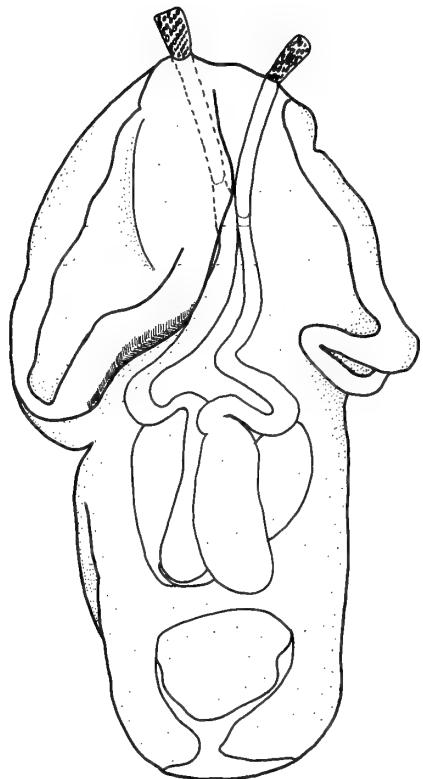


Fig. 12 *Nybelinia akanariae* sp. nov. Scolex from *Xiphiurus capensis*. Scale bar=150 µm.

atrium ventro-submarginal, in anterior third of the segment; genital pores alternate irregularly. Cirrus sac elongate and slender, in final segments $55\text{--}90 \times 1200\text{--}1330$ in size, directed anteromedially, parallel to anterior end of the proglottids; sac thin-walled; cirrus unarmed and coiled within sac. Other internal structures not seen.

REMARKS. The present specimen belongs to subgroup IAa of Palm *et al.* (1997) and resembles, with a rose-thorn-shaped basal and metabasal tentacular armature, *N. anthicosum*, *N. palliata*, *N. strongyla*, *N. riseri*, *N. sphyrnae* and *N. thrysites*. A comparison with the type material of *N. anthicosum* and *N. palliata*, deposited at the U.S. National Parasite Collection, Beltsville, revealed differences in oncotaxy. *N. strongyla* has a much larger TW=55 and SL=2300 and larger hooks, and *N. riseri* has smaller hooks together with a larger TW and a different scolex form (Dollfus, 1960). *N. sphyrnae* and *N. thrysites* also differ in hook and scolex form/size (see Beveridge & Campbell, 1996). Thus, the present specimen represents a new species, *Nybelinia schmidtii* sp. nov.

ETYMOLOGY. The new species is named after the parasitologist G. D. Schmidt.

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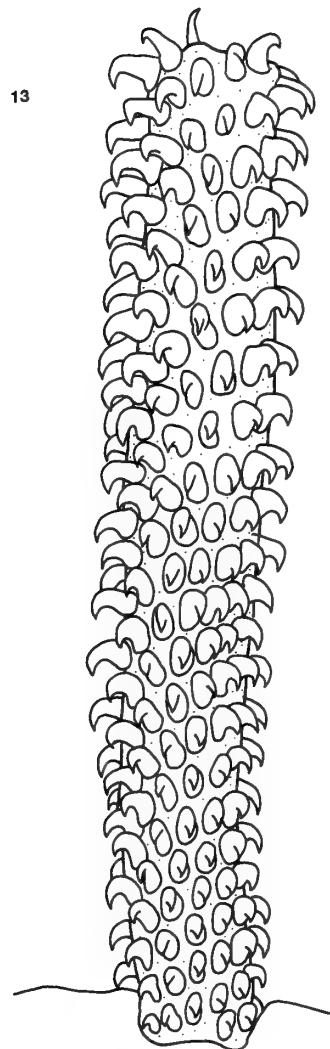


Fig. 13 *N. akanariae* sp. nov. from *X. capensis* Homeomorphous basal and metabasal armature. Scale bar=20 µm.

8. *Nybelinia scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) comb. nov. (*Tentacularia scoliodoni*) (Figs 16–17)

MATERIAL EXAMINED. BMNH 1976.11.5.42–43, R. van der Elst leg., 1 adult from the gut of *Carcharhinus limbatus*, South Africa. Additional material: NHMV 2111, A.E. Shipley leg., 1 adult from *Glypis gangeticus* (=*Carcharhinus gangeticus*), India.

DESCRIPTION (Fig. 16–17). Measurements: SL=667; SW=320; pbo=267; pv=227; pb=144; vel=267; BL=133 (125–144); BW=59 (56–64); BR=2.2:1; SP=1.9:1.6:1. The tentacles are 173–200 long and a basal tentacle swelling is absent. The TW varies along the tentacle; at the most proximal part of the basal armature, TW=14–17; at the basal armature, TW=23–25; at the apical armature, TW=12–13. The tentacle sheaths are straight (TSW=18–21), prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The metabasal armature is homeoacanthous, homeomorphous,

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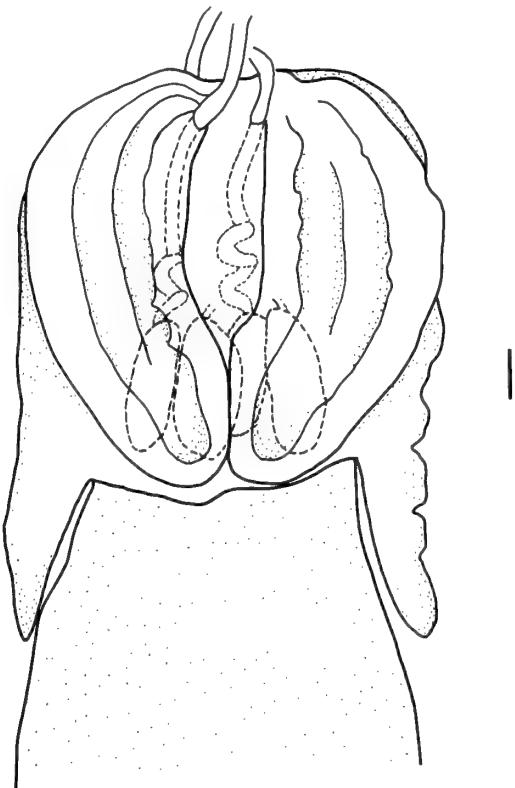


Fig. 14 *Nybelinia schmidti* sp. nov. Scolex from *Isurus glaucus*. Scale bar=100 µm.

and a distinctive basal armature is present (Fig. 17). The basal armature consists of about 11 rows with compact rose-thorn-shaped hooks, increasing in size (row 1–5: L=3.5–5.6, B=3.5–4.9, and row 6–11: L=7–9.8, B=5.6–8.4). From rows 12–14, the hook form changes to long, spiniform metabasal hooks (L=22–26) with a small base (B=7.7–10.5); hsr basal=6–7, hsr metabasal=4–5.

No complete strobila is present. The first acraspedote proglottids are wider than long (330 × 50) and slightly increasing in size (490 × 205). Other internal structures were not seen.

REMARKS. Palm & Walter (1999) considered *Nybelinia* (*Tentacularia*) *scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharan, 1996) as a species of uncertain status due to an incomplete original description and a strong similarity to *Nybelinia indica* Chandra, 1986. However, the present specimen confirms the validity of *Tentacularia scoliodoni*, and assigns the species to the genus *Nybelinia* Poche, 1926. Though the scolex measurements of the present specimen are smaller and the scolex and bulb ratios show differences to those given in the original description, the tentacular armature corresponds in detail with *N. scoliodoni*. The drastic change in form from rose-thorn shaped basal to spiniform metabasal hooks, with a size between L=8–11 in the basal and L=30, B=3 in the metabasal armature as given by Vijayalakshmi *et al.* (1996), is unique within the genus. As with the scolex size, the hooks of the present specimen are slightly smaller than those of the original description. However, Vijayalakshmi *et al.* (1996, figure 8) demonstrated minute hooks on the basal part of the tentacle, similar to those in rows 1–5 of the present specimen, and also indicated the characteristic change in TW along the tentacles (figure 7). The known range of distribution is extended to South Africa, and *Carcharhinus*

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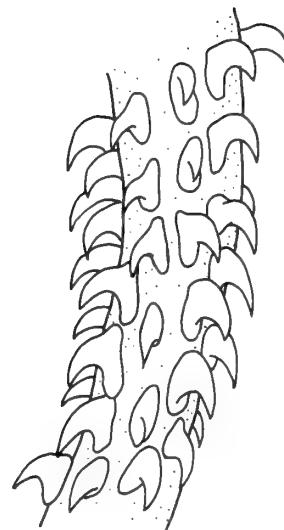


Fig. 15 *N. schmidti* sp. nov. Homeomorphous basal and metabasal armature. Scale bar=10 µm.

limbatus is a new host for *N. scoliodoni*. Under the co-type material of *Nybelinia perideraeus* (Shipley & Hornell, 1906), slide No. 12f, an adult *N. scoliodoni* with an incomplete strobila was found. The scolex size and tentacular armature corresponds to the material deposited at the BMNH. Thus, *Glypis gangeticus* represents a new host for *N. scoliodoni*, and this finding supports its occurrence in Indian Ocean waters.

N. scoliodoni has similarities with *N. indica* Chandra, 1986, which was also described from the Indian Ocean. *N. indica* differs due to its larger size, a large ppb, a larger TW in the basal part of the tentacle and a more gradual change in hook form along the tentacles (Chandra, 1986). In contrast to this, the form of the hooks as well as their size show similarities to both *N. scoliodoni* and the present specimen. The real identity of *N. indica* and a possible synonymy with *N. scoliodoni* cannot be decided until a re-examination of the type material is undertaken. Therefore, both species remain valid, and on the basis of the above described characters, the present specimen is identified as *N. scoliodoni*. The present specimen was obtained from a carcharhinid shark from South Africa, which further extends the distribution of the species from the Indian to the South African coast.

Palm (1997b) found similar small *Nybelinia* specimens (SL=640, SP=3.6:2:1) with a similar tentacular armature (L=5–24, rose-thorn shaped basal and spiniform metabasal hooks (Fig. 18; figure 17 in Palm, 1992) in *Pseudupeneus maculatus* from the North-East Brazilian coast and described the specimens as *N. indica* with a homeomorphous metabasal armature. The drawing of the tentacular armature of one of the specimens as given in Palm (1992) shows similar hooks as demonstrated for the present specimens. However, its affinities with *N. indica* or *N. scoliodoni* cannot be decided at present (see above).

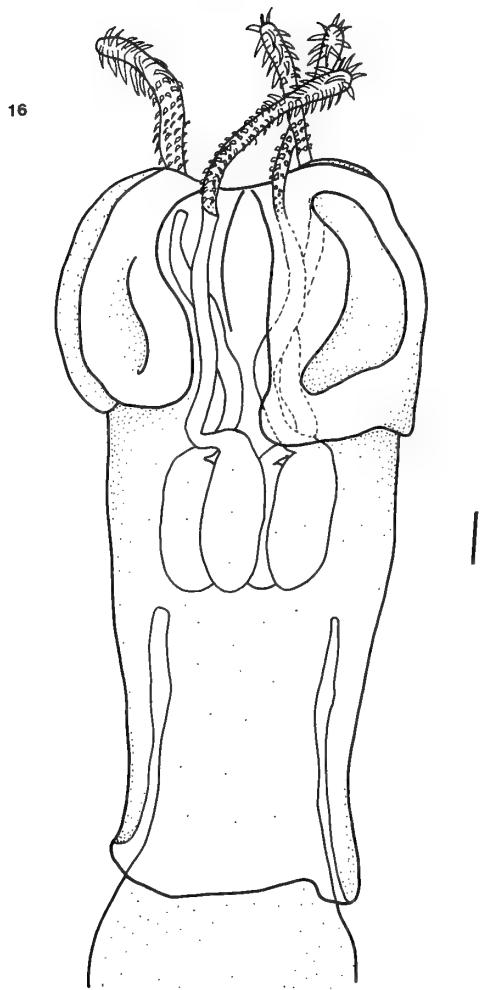


Fig. 16 *Nybelinia scoliodoni*. Scolex from *Carcharhinus limbatus*. Scale bar=50 µm.

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Fig. 17 *N. scoliodoni*. Homeomorphous basal and metabasal armature consisting of rose-thorn shaped and falcate hooks. Scale bar=20 µm.

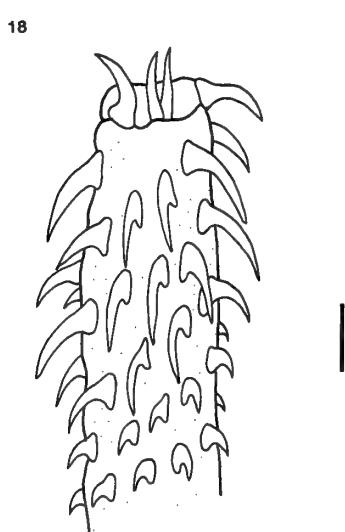


Fig. 18 *N. indica*. Homeomorphous basal and metabasal armature (Palm 1992). Scale bar=20 µm.

9. *Nybelinia* sp.

MATERIAL EXAMINED. BMNH 1979.9.13.94, leg. R. van der Elst, 2 postlarvae from the kidney of *Coryphaena hippurus*, Cape Vidal, South Africa.

DESCRIPTION. The following measurements were taken: SL=1172, 1228; SW=775, 907; pbo=888, 850; pv=624, 548; pb=252, 257; ppb=33, 38; app=364, 294; vel=186; 150; BL=246 (234–247), 251 (224–266); BW=99 (84–112), 114 (112–117); BR=2.5:1, 2.2:1; SP=3.5:2.5:1, 3.3:2.1:1. The tentacles are long, TL=586–606, 583 and slender, TW=32.8–35.2, 32.8–35.2 and a basal swelling is absent. The tentacle sheaths are sinuous; TSW=32.8–37.6, 32.8–37.6. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous and a characteristic basal armature is absent. The small and rose-thorn shaped hooks are of the same size along the tentacle, L=8.0–10.4, 8.0–10.4; B=8.8–11.0, 8.8–11.0; hsr=6.

REMARKS. The present specimens resemble *N. oodes* and *N. riseri* as described by Dollfus (1960), both species having small rose-thorn shaped homeomorphous hooks along the tentacle. *N. riseri* has a

different scolex form (see above), larger TW and TSW and the tentacular hooks are larger. In contrast, the morphological measurements SL, TL, TW, TSW and the small size and form of the hooks are similar to *N. oodes* (SL=920, TL=400–500, TW=24–27, TSW=40–48, B=9.3–10.6) as described by Dollfus (1960). Examination of the type material revealed a slightly heteromorphous tentacular armature for *N. oodes*. This neither corresponds to the original description (see Dollfus, 1960, Figs 36–37) nor to the present specimens. Thus, the present postlarvae should not be assigned to *Nybelinia oodes* and might represent a new *Nybelinia* species. This needs to be decided after re-description of the *Nybelinia* type material deposited at the MNHN Paris.

***Heteronybelinia* gen. nov.**

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, 4 triangular bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and the scolex. 4 tentacles emerging from bulbs, retractor muscle originates at base of bulbs. 4 proboscis of variable length and width, armed with hooks; metabasal tentacular armature homeoacanthous with heteromorphous hooks on different tentacle surfaces. Basal hooks heteromorphous, characteristic basal armature absent or present. Cirrus unarmed, cirrus sac alternates irregularly.

TYPE SPECIES. *Heteronybelinia estigmata* (Dollfus, 1960).

OTHER SPECIES. *H. alioiotica* (Dollfus, 1960), *H. cadenati* (Dollfus, 1960), *H. elongata* (Shah & Bilquees, 1979), *H. eureia* (Dollfus, 1960), *H. heteromorphi* sp. nov., *H. karachii* (Khurshid & Bilquees, 1988), *H. minima* sp. nov., *H. nipponica* (Yamaguti, 1952), *H. perideraeus* (Shipley & Hornell, 1906), *H. punctatissima* (Dollfus, 1960), *H. robusta* (Linton, 1890), *H. rougetcampanae* (Dollfus, 1960), *H. senegalensis* (Dollfus, 1960), *H. yamagutii* (Dollfus, 1960), all formerly belonging to the genus *Nybelinia* Poche, 1926.

COMMENT. This new genus comprises subgroup II in Palm *et al.* (1997).

10. *Heteronybelinia elongata* (Shah & Bilquees, 1979) comb. nov. (Figs 19–25)

MATERIAL EXAMINED. Types BMNH 1989.5.18.5, Shah & Bilquees leg., 1979, 2 postlarvae from *Pellona elongata*, Pakistan; BMNH 1980.6.23.13, A. Roy leg., 1 postlarva from the gonads of *Lepturacanthus savala*, Hooghly estuary, India. Other material not measured: BMNH 1992.7.1.193–196, A. Roy leg., postlarva from *Lepturacanthus savala*, Sugar Island, Bay of Bengal.

DESCRIPTION. The scolex morphology of the type material of *H. elongata* (Shah & Bilquees, 1979) from *Pellona elongata*, together with the scoleces and armature of specimens from *Lepturacanthus savala*, are given in Figs 19–25. The type material is re-described as follows (Fig. 19): The scolex is about 2 mm large, but is variable in size, SL=2173, 2362 (a third specimen on the same slide: 1740); SW=1000, 1021; pbo=982, 964; pv=1021, 1021; pb=536, 548; ppb=227, 252; app=605, 624; vel=302, 300; BL=514 (490–536), 525 (510–548); BW=130 (125–135), 128 (112–144.8); BR=3.9:1, 4.1:1; SP=1.8:1.9:1. The tentacles are long and slender with a TW metabasal =15.2–17.6; TW basal= 17.6–20.8, diminishing slightly towards the metabasal part of the tentacle. A basal tentacular swelling is absent. Prebulbar organs were absent, muscular rings around the basal part of the tentacle sheaths were visible in some

specimens (see also Fig. 22). Tentacle sheaths straight; retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous, and a characteristic basal armature is absent (see Figs 23–24). The form of the hooks is rose-thorn shaped. The hook size in the metabasal region (see Fig. 25) ranged between L=11.2–12.8; B=9.2–11.2, 11.2–12.8 (bothridial) and L=9.2–11.2, 8.8–11.2; B=5.6–7.2, 7.2–9.2 (antibothridial), and the hook size in the basal region of the tentacle was between L=9.2–11.2; B=9.2–11.2 (bothridial) and L=5.6–7.2; B=4–5.6, 5.6–7.2 (antibothridial); the hook size increases only on the antibothridial tentacle surface; hsr=6–7.

Postlarvae from *Lepturacanthus savala* (Fig. 20): Measurements: SL=1360; SW=642; pbo=662; pv=605; pb=397; ppb=61; app=257; vel=233; BL=387 (377–397), BW=91 (89–94); BR=4.2:1; SP=1.7:1.5:1. The tentacles are long and slender with a TW metabasal =20.8–24; TW basal= 24–27.2. A basal tentacular swelling is absent. Prebulbar organs are absent and muscular rings around the basal part of the tentacle sheaths are present; TSW= 32.8–36, straight; retractor muscles originate at the basal part of the bulbs.

The hook size in the metabasal armature ranged between L=9.6–11.2; B=9.2–11.2 (bothridial) and L=8.0–9.2; B=5.6–7.2 (antibothridial), and the hook size in the basal part of the tentacle was between L=7.2–9.2; B=7.2–9.6 (bothridial) and L=4–5.6; B=5.6–7.2 (antibothridial); The hook size increases mainly on the antibothridial tentacle surface towards the metabasal part of the tentacle; hsr=6–7.

Scoleces, muscular ring and the tentacular armature of specimens BMNH 1992.7.1.193–196 are shown in Figs 21–25.

REMARKS. The type material of *N. elongata* from *Pellona elongata* is re-described, as well as additional material of the same species collected from *Lepturacanthus savala*. Though the material differs in absolute morphometrical values, BR, SP and the tentacular armature are very similar. Recently, Palm & Walter (1999) examined the type material of *N. perideraeus* from the Natural History Museum Vienna and re-described the species as having a homeoacanthous, heteromorphous tentacular armature. The authors considered *N. dakari* to be synonymous with *N. perideraeus*, characterised by tentacular hooks of similar size in the basal and metabasal part of the tentacle. The present material of *N. elongata* also has very similar scolex measurements as well as similar tentacular hooks to those of *N. perideraeus*. However, the hook size increases on the antibothridial tentacle surface towards the metabasal part of the tentacle. Thus, until further material becomes available, both species are considered valid. The position of *N. elongata* changes from subgroup IAb to IIAb in Palm *et al.* (1997).

N. elongata appears to have a high degree of scolex variability, e.g. the SL ranges between 1739 and 2362 in 3 different specimens on the same slide. As well as similarities between *N. elongata* and *N. perideraeus*, a close relationship can be seen to other species from subgroup IIAb, all having a similar armature with similar sized tentacular hooks. It is recommended that the type material of species in subgroup IIAb described by Dollfus (1960) be compared with *N. perideraeus* and *N. elongata* to clarify the species identity within this subgroup (also see below).

11. *Heteronybelinia estigmata* (Dollfus, 1960) comb. nov. (Figs 26–28)

MATERIAL EXAMINED. BMNH 1976.11.5.42–43, R. van der Elst leg., 1 adult from the gut of *Carcharhinus limbatus*, South Africa; BMNH 1985.11.8.63–64, R. van der Elst leg.; 11.05.1984, 1 adult from *Carcharhinus leucas*, Richards Bay, South Africa; BMNH

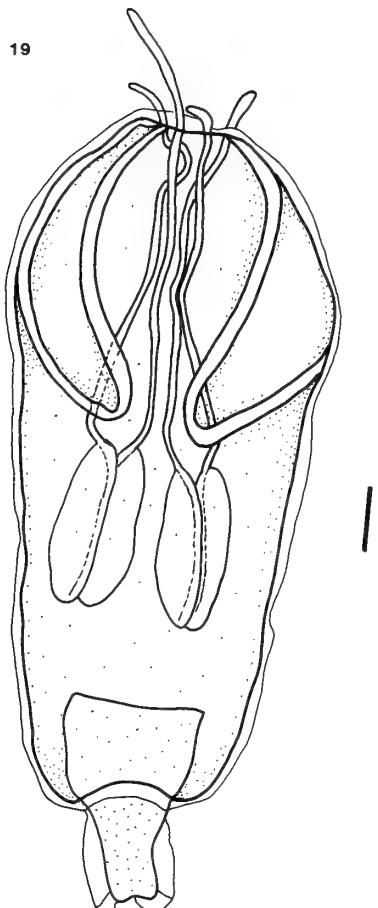


Fig. 19 *Heteronybelinia elongata*. Scolex from *Pellona elongata*. Scale bar=200 μm .

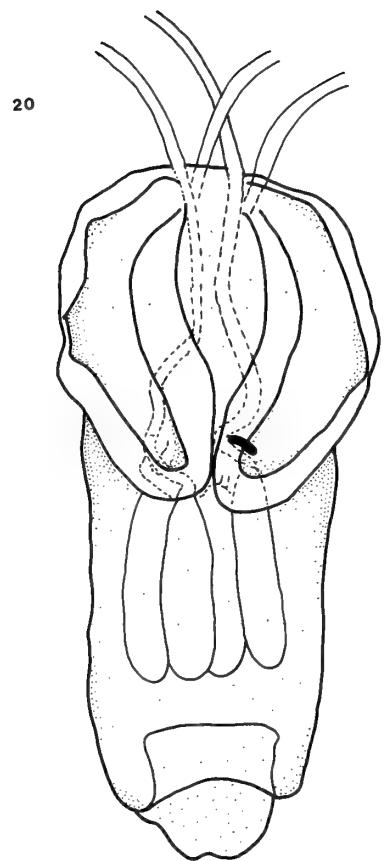


Fig. 20 *H. elongata*. Scolex from *Lepturacanthus savala*. Scale bar=100 μm .

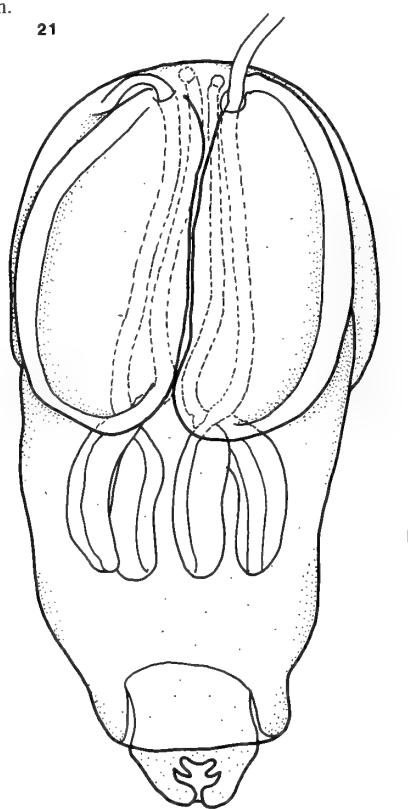


Fig. 21 *H. elongata*. Scolex from *L. savala*. Scale bar=100 μm .

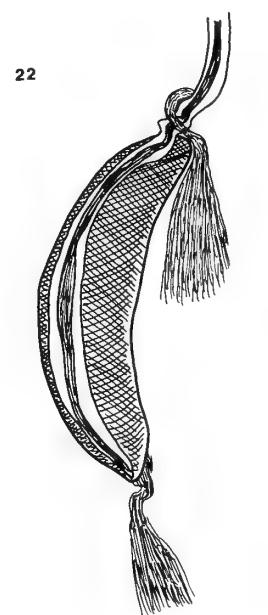


Fig. 22 *H. elongata* from *L. savala*. Muscular ring around tentacle sheath. Scale bar=50 μm .

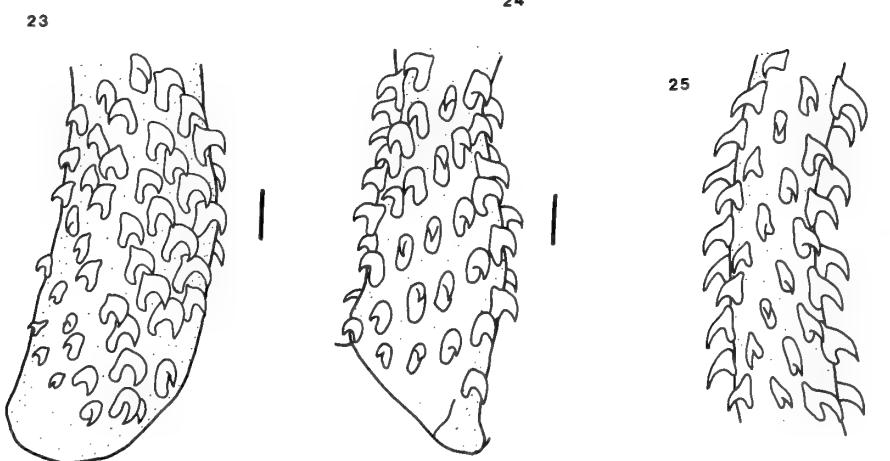


Fig. 23 *H. elongata* from *L. savala*. Heteromorphous basal armature, external surface. Scale bar=10 µm.

Fig. 24 *H. elongata* from *L. savala*. Heteromorphous basal armature, bothridial surface, external face on left hand side. Scale bar=10 µm.

Fig. 25 *H. elongata* from *L. savala*. Heteromorphous metabasal armature, external surface. Scale bar=10 µm.

1996.8.19.1–3, D.T.J. Littlewood leg., Aug. 1995, 1 postlarva from the stomach of a kingfish, Port Royal, Kingston, Jamaica.

DESCRIPTION. The scolex of a specimen from *C. limbatus* is shown in Fig. 26. Measurements: SL=1210, 1134, 1000; SW=700, nm, 493; pbo=700, 642; 500; pv=510, 473, 500; pb=448, 330; 307; ppb=95, 75, 27; vel=170, 232, 160; BL=442 (428–448), 326 (312–331), 287 (280–294); BW=128 (126–130), 104 (84–107), 81 (75–92); BR=3.5:1, 3.2:1; 3.5:1; SP=1.6:1.1:1, 1.9:1.4:1, 1.6:1.6:1. The tentacles are long and slender, with TW=27–30; 23–28, 20–22; TSW increases in size towards the base of the tentacles (24–27, 22–28, 29–32), a basal tentacular swelling is absent. Prebulbar organs are absent and muscular rings around the basal part of the tentacle sheaths are present in specimens from *Carcharhinus* spp. The retractor muscles originate at the base of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous, and a characteristic basal armature is absent (Figs 27–28). The hooks diminish in size towards the basal part of the tentacle, the hooks are rose-thorn shaped on both sides of the tentacles. The single hook sizes of the three specimens in the metabasal armature were L=9.2–11.2, B=9.2–11.2; L=10.4–12, B=10.4–12; L=9.2–10.5, B=9.3–10.5 (mean L bothridial=10.4) and L=7.2–9.6, B=7.2–9.6; L=9.6–10.4, B=10.4–12; L=7.4–8, B=7.4–8 (mean L antithothridial=8.7), and in the basal part of the tentacle L=7.2–9.2, B=7.2–9.2; L=7.2–8.8, B=7.2–8.8; L=7.2–8, B=7.2–8 (bothridial) and L=5.6–7.2, B=5.6–7.2; L=5.6–7.2, B=4.8–5.6; L=5–6, B=5–6 (antithothridial); hsr=6–7.

The slightly stained strobila of the specimen from *Carcharhinus limbatus* consists of about 190 acraspedote proglottids. Proglottids wider than long and increasing in size (about 50th proglottid: 55–60 × 475–485; 100th: 185–210 × 560–585; 150th: 360–420 × 755–780; 190th: 670–730 × 840–900). 80–90 testes in a single layer, 33–55 (between 100th and 150th segments) and 50–65 (final segments) in diameter. Genital pores ventro-lateral, in the anterior half near the middle of the proglottids, alternate irregularly; cirrus sac elongate, directed anteromedially, reaching the anterior end of the proglottids; increasing in size, from 50–60 × 290–350 until 85–90 × 345–365 in last segments. Other internal structures not seen. The acraspedote proglottids of the specimen from *Carcharhinus leucas* vary in size,

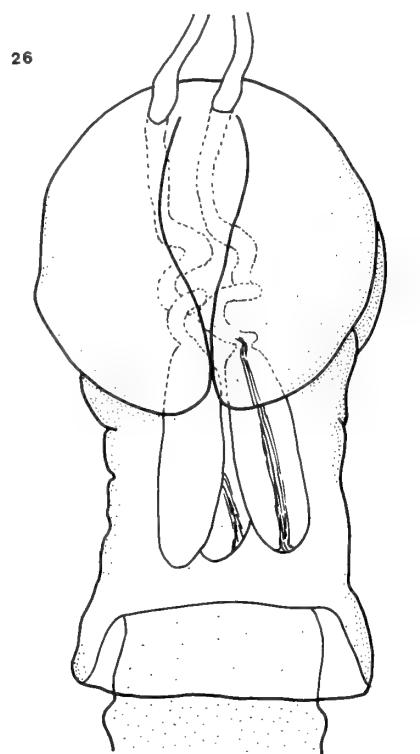


Fig. 26 *Heteronybelinia estigmene*. Scolex from *Carcharhinus limbatus*. Scale bar=100 µm.

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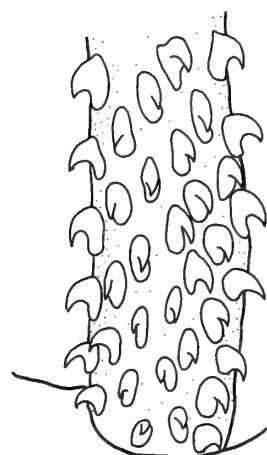


Fig. 27 *H. estigmena* from *C. limbatus*. Heteromorphous basal armature, bothridial surface. Scale bar=10 µm.

Fig. 28 *H. estigmena* from *C. limbatus*. Heteromorphous metabasal armature, antibothridial surface. Scale bar=10 µm.

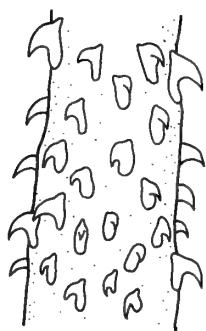
depending on contraction (anterior segments: 80 × 330–20 × 520), final segments 300–370 × 860–880; testes 33–55 in diameter.

REMARKS. The present specimens are most similar to *H. alloiotica*, *H. punctatissima* and *H. estigmena*, which were considered as belonging to subgroup IIa by Palm *et al.* (1997), comprising species having a heteromorphous tentacular armature with hooks diminishing in size towards the basal part of the tentacle, and no characteristic basal armature. Dollfus (1960) described 6 species, *H. dakari*, *H. estigmena*, *H. punctatissima*, *H. senegalensis*, *H. alloiotica* and *H. cadenati*, with a heteromorphous tentacular armature and small hooks of about 10–11 µm (bothridial) and 8 µm (antibothridial). All these species have a very similar scolex and hook morphology, mainly differing from each other by a different bulb ratio and different scolex proportions. Palm & Walter (1999) proposed the synonymy of *Nybelinia dakari* Dollfus, 1960 with *H. perideraeus*, differing from the other species in having a basal armature of similar size to the metabasal armature. Though Dollfus (1960) stated that the bulb ratio of *H. dakari* was small (about 2.5:1), his drawing (figure 43) indicates a ratio of about 4. His bulb measurements of 0.380–0.386 × 0.96–0.100 mm are faulty (0.96 might stand for 0.096), which would also indicate a bulb ratio of about 3.9, thus, corresponding to the ratio of *H. perideraeus* (see Palm & Walter, 1999). *H. senegalensis*, *H. alloiotica* and *H. cadenati* also have a bulb ratio of about 4, and *H. punctatissima* differs from *H. estigmena* by having a slightly different bulb ratio and different scolex dimensions (2.1:1.6:1 vs 1.5:1:1). However, these two species appear to be very similar, and the tentacular armature of *H. alloiotica* (Figs 29–30), which was re-described by Palm (1995) from *Carcharhinus limbatus* from the Gulf of Mexico, also corresponds with that of the present material. The present finding represent 3 new host and locality records for *H. estigmena*.

This and a previous study (Palm & Walter, 1999) demonstrate wide intraspecific variability in scolex morphology within several species of *Nybelinia* (see also *H. africana*) and *Heteronybelinia*, similar to that described earlier for other tentaculariid genera *Tentacularia* and *Hepatoxylon* (Palm, 1995). Additionally, Palm *et al.* (1997) pointed out the dubious value of the 2 characters tentacle width and bulb ratio, which Dollfus used to distinguish the above 6

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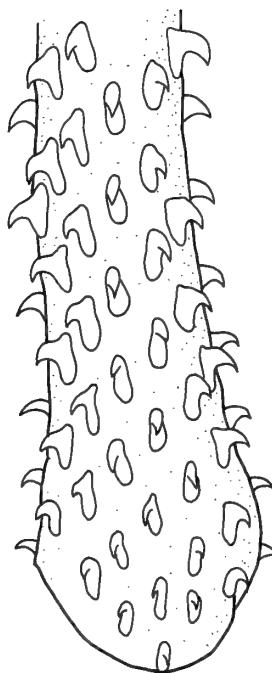


Fig. 29 *Heteronybelinia alloiotica* from *Carcharhinus limbatus*.

Heteromorphous basal armature, bothridial surface. Scale bar=10 µm.

Fig. 30 *H. alloiotica*. Heteromorphous metabasal armature, antibothridial surface. Scale bar=10 µm.

species. The identification of the present specimens as *Heteronybelinia estigmena* needs to be confirmed by re-examining the type material of the above mentioned species. The possibly synonymy of all these species has to be kept in mind.

Heteronybelinia cf. *estigmena* (Dollfus, 1960) comb. nov.

MATERIAL EXAMINED. BMNH 1989.1.18.2, R. Bray leg., 14.01.1971, Cirolana, Atlantic Ocean off Morocco, 33°43'N, 8°38'W, 222–236 m. 1 postlarva from *Scomber scolias*.

REMARKS. Due to its scolex morphology and the homeoacanthous, heteromorphous tentacular armature with a basal hook size of L=8.8–10.4, B=8.8–10.4 (bothridial) and L=5.6–7.2, B=5.6–7.2 (antibothridial), the present specimen was tentatively identified as *H. estigmena*. However, the partly invaginated metabasal armature and the unusual form due to fixation prevent precise identification. The presence of a muscular ring around the tentacle sheaths could not be demonstrated to be of any taxonomic significance.

12. *Heteronybelinia heteromorpha* sp. nov. (Figs 31–33)

MATERIAL EXAMINED. Holotype and paratype, BMNH 1982.4.26.282–284, R. van der Elst leg., 16.5.78, 2 adults from the stomach of *Sphyrna mokarran*, South Africa; Additional material: BMNH 1968.2.14.30–31, Gooding leg., 2 adults from *Sphyrna blochii*, Singapore.

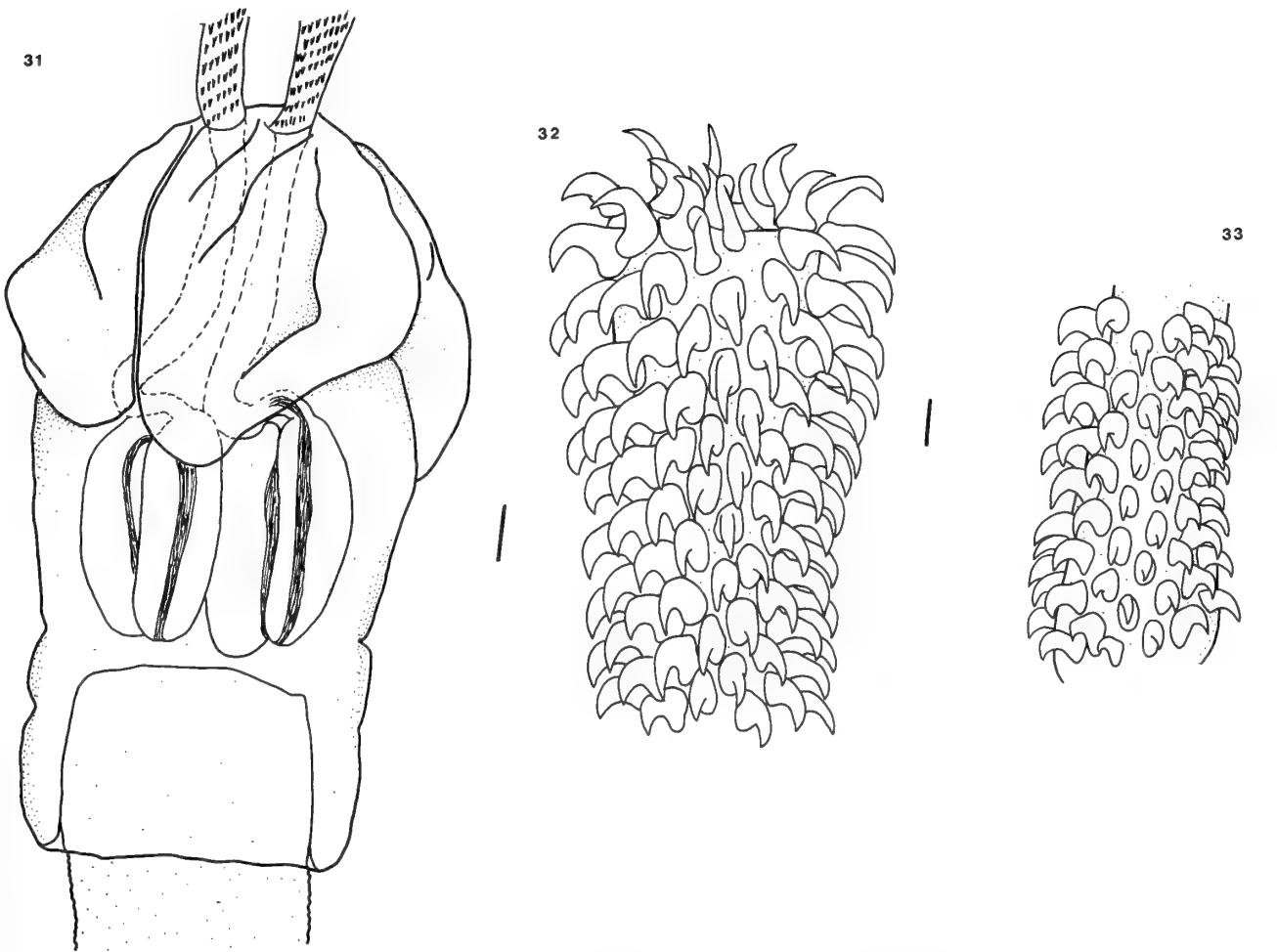


Fig. 31 *Heteronybelinia heteromorpha* sp. nov.. Scolex from *Sphyrna makorran*. Scale bar=100 µm.

Fig. 32 *H. heteromorpha* sp. nov. from *S. makorran*. Heteromorphous metabasal armature, bothridial (left hand side) and antibothridial (right hand side) surfaces. Scale bar=15 µm.

Fig. 33 *H. heteromorpha* sp. nov. from *S. makorran*. Heteromorphous basal armature, bothridial (left) and antibothridial (right) surfaces. Scale bar=15 µm.

DESCRIPTION (Figs 31–33). With the characters of the genus *Heteronybelinia*. Measurements: SL=1367, 1300, 1367, 1467; SW=833, 934, 800, 800; pbo=767, 734, 734, 867; pv=534, 500, 567, 506; pb=500, 447, 334, 427; ppb=20, 40, 105, 160; vel=333, 340, 317, 300; BL=437 (414–454), 404 (387–414), 327 (308–334), 405 (368–427); BW=154 (134–163), 181 (174–187), 158 (137–175), 176 (173–179); BR=2.8:1, 2.2:1, 2.1:1, 2.3:1; SP=1.5:1.1:1, 1.6:1.1:1, 2.2:1.7:1, 2.0:1.2:1. The tentacles are long, robust and increase in diameter towards the tip of the tentacle; TL=540 (27 rows of hooks), 480 (23 rows), 560 (25 rows), nm; TW basal=53–60, 53–60, 48–50, 52–54; TW apical=75–80, 65–70, 58–61, nm; a basal swelling is absent. The tentacle sheaths are straight; TSW=53–66, 45–54, 68–70, 69–74. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. A thickening, encircling more than half of the tentacle sheath near the entrance to the bulbs, is present. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous, and a characteristic basal armature is absent. The form of the hooks is rose-thorn shaped becoming more slender towards the tip of the

tentacle (Fig. 32). Similarly, the form changes from the bothridial to the antibothridial surface. The hook sizes of the metabasal tentacular armature for BMNH 1982.4.26.282–284 and 1968.2.14.30–31 are as follows: above 22th row, L=24–28, B=19–21; L=25–28, B=15–17 (bothridial) and L=28–32, B=12–15; L=30–32, B=12–15 (antibothridial); about 14th row, L=22–25, B=16–17; L=21–23, B=16–17 (bothridial) and L=25–28, B=11–15; L=30–32, B=12–15 (antibothridial); The basal hooks (Fig. 33) ranged between L=16–18 and B=10–12; hsr=7–8.

The strobila of the largest specimen of BMNH 1982.4.26.282–284 consists of about 350 acraspedote proglottids. The proglottids are uniform in measurements, much wider (934–1034) than long (50–134). Proglottids of smaller specimens measured about 600 in width and 100 in length. The genital pores alternate irregularly; cirrus sac 35–40 × 140–160. Small testes (25–40 in diameter) and vitellaria (10–15); other internal structures not seen.

REMARKS. The present specimens belong to subgroup IIa (Palm *et al.*, 1997), with a heteromorphous armature and hooks increasing in size towards the metabasal part of the tentacle. The large hook size

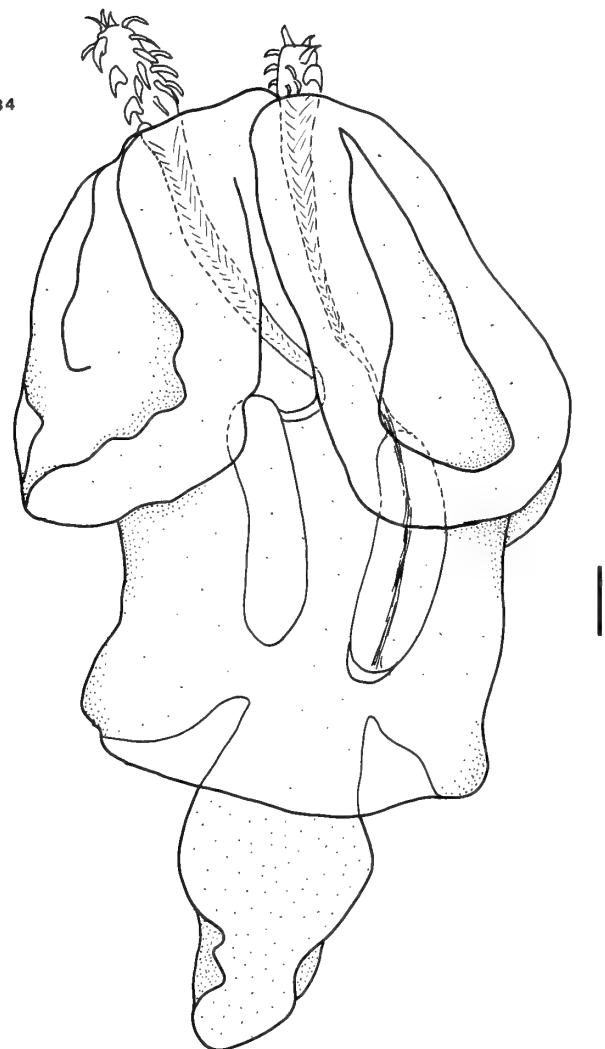


Fig. 34 *Heteronybelinia minima* sp. nov.. Scolex from *Harpodon nehereus*. Scale bar=50 µm.

and the tight arrangement of the hooks along the tentacle is characteristic for the specimens, and together with the heteromorphous armature, the character combination corresponds only with *Heteronybelinia eureia* as described by Dollfus (1960). Though the morphometrical data correspond, the drawings of the tentacular armature of *H. eureia* as given by Dollfus (1960, figures 33–35) indicate more widely spaced and more slender hooks than was observed in the present specimens. This was confirmed by examination of the type material at the MNHN Paris. Additionally, the description by Dollfus, based on postlarvae, precludes comparison of the strobilar characters. Thus, the present specimens represent a new species, *Heteronybelinia heteromorpha* sp. nov. Other similar species with a compact hook pattern are *Nybelinia queenslandensis* and *N. strongyla* (see Jones & Beveridge, 1998, Dollfus, 1960). However, these species have a homeomorphous tentacular armature.

ETYMOLOGY. The new species is named after the characteristic heteromorphous armature.

13. *Heteronybelinia minima* sp. nov. (Figs 34–38)

MATERIAL EXAMINED. Holotype and paratype, BMNH 1980.12.2.1, A. Roy leg., 14.09.79, 2 postlarvae from *Harpodon*

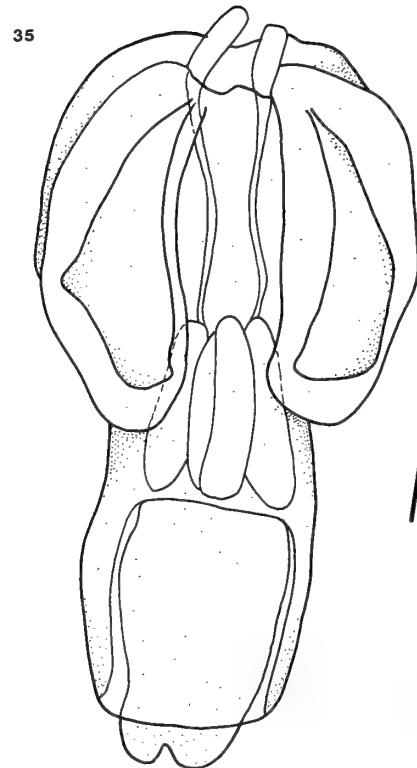


Fig. 35 *H. minima* sp. nov.. Scolex from *Polynemus paradiseus*. Scale bar=100 µm.

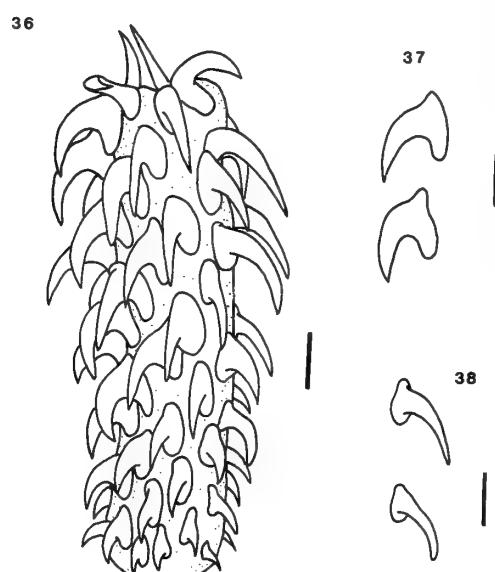


Fig. 36 *H. minima* sp. nov. from *P. paradiseus*. Heteromorphous metabasal armature, bothridial (left hand side) and antibothridial (right hand side) surfaces. Scale bar=15 µm.

Fig. 37 *H. minima* sp. nov., hooks on bothridial surface. Scale bar=15 µm.

Fig. 38 *H. minima* sp. nov., hooks on antibothridial surface. Scale bar=15 µm.

nehereus, Houghly estuary, India. Other postlarvae identified as *H. minima* sp. nov.: BMNH 1980.6.23.13 from *Polynemus* sp.; 1980.6.23.14, A. Roy leg., *Polynemus* sp., Houghly estuary, India (4 postlarvae); 1992.7.1.189 from *Harpodon nehereus*; 1992.7.1.190–192, A. Roy leg., *Polynemus paradiseus*, Sugar Island, Bay of Bengal (5 postlarvae).

DESCRIPTION. With the characters of the genus *Heteronybelinia*. The scolex of the holotype as well as the scolex and basal and metabasal tentacular armature of a specimen from *P. paradiseus* are shown in Figs 34 and 35–38 respectively. The scolex is small, differing in size and shape between specimens. Measurements (from types 1980.12.2.1): SL=706, 926; SW=386, 642; pbo=427, 454; pv=267, 397; pb=200, 252; app=280, 270; vel=84, 186; BL=191 (187–200), 237 (229–252); BW=54 (43–66), 83 (74–89); BR=3.5:1, 2.9:1; SP=2.1:1.3:1, 1.8:1.6:1. The tentacles are long, in inverted condition nearly reaching the apical end of the bulbs, with a TW=23–28; TW increases towards the tip of the tentacles, a basal tentacular swelling is absent. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the base of the bulbs (Fig. 34).

The tentacular armature is homeoacanthous, heteromorphous and a characteristic basal armature is absent (Figs 36–38). The hooks diminish in size towards the basal part of the tentacle, the form of the hooks differs from compact and rose-thorn shaped (bothridial) to falcate hooks with a stout base (antibothridial). The hook size in the metabasal armature ranged between L=20.8–24; B=15.2–16.8 (bothridial) and L=24–27.2; B=5.6–7.2 (antibothridial), and the hook size in the basal part of the tentacle was between L=12–17.6; B=7.2–12 (bothridial) and L=15.2–17.6; B=7.2–8.8 (antibothridial); hsr=6.

ETYMOLOGY. The new species is named for its small size.

REMARKS. *H. minima* sp. nov. is easily identifiable by its small scolex size and the characteristic tentacular armature. The present specimens from *Harpodon nehereus*, *Polynemus paradiseus* and *Polynemus* sp. clearly demonstrate a heteromorphous armature, where the hook form changes from rose-thorn shaped to falcate hooks, giving the tentacles a heteroacanthous appearance. However, the quincunx formation of the hooks is still recognisable. The absence of a characteristic basal armature places the species in subgroup IIa of Palm *et al.* (1997).

14. *Heteronybelinia robusta* (Linton, 1890) (Figs 39–41)

MATERIAL EXAMINED. BMNH 1976.11.5.42–43, R. van der Elst leg., 1 adult from the gut of *Carcharhinus limbatus*, South Africa. Additional material: USNPC 7727, E. Linton leg., 3 adults from *Dasyatis centroura*, Woods Hole, USA.

DESCRIPTION (Figs 39–41). With the characters of the genus *Heteronybelinia*. Measurements: SL=1020; SW=699; pbo=510; pv=377; pb=257; vel=294; BL=246 (233–257); BW=82 (79–84); BR=3:1; SP=2:1.5:1. The tentacles are slender, and increase in width towards the metabasal and decrease towards the apical part of the tentacle; TW=24–30; a basal swelling is absent. The tentacle sheaths have two spiral coils; TSW=24–27. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous and a characteristic basal armature is absent. The form of the hooks changes slightly from compact and rose-thorn shaped (bothridial) to more slender hooks with a stout base (antibothridial) (Fig. 40). The

hook size in the metabasal armature ranged between L=11.7–12.5; B=7.2–9.2 (bothridial) and L=13.0–14.0; B=5.6–7.2 (antibothridial), and hooks of the basal part of the tentacle (Fig. 41) were minute, between L=5.6–7.2; B=5.6–7.2 (bothridial) and L=4–5.6; B=4–5.6 (antibothridial), continuously increasing towards the tip; hsr=6–7.

The strobila of the small specimen consists of 71 acraspedote proglottids. Measurements of the proglottids were as follows: proglottid 20: length=48, width=320; proglottid 48: length=140, width=400; proglottid 62: length=490, width=656; proglottid 70: length=610, width=746. Genital pores ventro-lateral, in the anterior third of the proglottids, alternate irregularly; cirrus sac elongate, directed anteromedially, reaching the anterior end of the proglottids. Other internal structures were not seen.

REMARKS. The present specimen corresponds to 3 specimens described as *N. robusta* by Linton (1924). Scolex measurements and the characteristic tentacular armature lie within the same range. Thus the present specimen is identified as belonging to the same species. However, as the type material of *N. robusta* is not available at the USNPC, the taxonomy of *N. robusta* still needs to be clarified.

There are several species which have rose-thorn-shaped heteromorphous hooks along the tentacle. *H. robusta* differs from all adequately described species due to the small scolex size with minute basal hooks, continuously increasing in size from 5 to 12.5 (bothridial) and 4 to 14 µm (antibothridial). The general hook form remains rose-thorn shaped along the tentacles. Thus, the present specimen belongs into subgroup IIa of Palm *et al.* (1997).

15. *Heteronybelinia yamagutii* (Dollfus, 1960) nov. comb. (Fig. 42–44)

MATERIAL EXAMINED. BMNH 1976.11.5.41, R. van der Elst leg., 1 adult from the stomach of *Sphyrna lewini*, South Africa.

DESCRIPTION. *Nybelinia yamagutii* was described in detail by Dollfus (1960, see figures 1–5) and Palm *et al.* (1997). The following measurements were taken: SL=2646; SW=1080; pbo=1134; pv=1000; pb=1455; vel=140; BL=1430 (1418–1455); BW=236 (220–247); BR=6.1:1; SP=0.8:0.7:1. The tentacles are long and slender and diminish in size along the tentacle; TW metabasal=90–98, TW apical=66–75. A basal tentacular swelling is not present. The tentacle sheaths are sinuous; TSW=51–56. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, heteromorphous, and a characteristic basal armature with bill-hooks is present. The hooks of the metabasal armature are different in shape and size on bothridial and antibothridial tentacle surfaces. The form of the hooks is described in detail in Dollfus (1960). The hook size in the metabasal armature was between L=69–75 (bothridial) and L=60–65 (antibothridial). The size of the basal hooks was between L=18–23. The bill-hooks were in rows 3–4 with a total length of 41–46.

The 12.5 cm long worm has a craspedote strobilar with several hundred segments increasing in size (Figs 42–44); last proglottid with rounded proximal end. The size varies in the first 2 cm of the strobila between 70–100 long and 300–420 wide, from 4–5 cm between 195–220 and 780–900 (Fig. 42), from 7–8 cm between 360–420 and 1260–1400 (Fig. 43), and at the final proglottids between 360–400 and 1680–1820 (Fig. 44). In mature proglottids, the elongate cirrus sac is directed anteromedially, and alternates irregularly (Fig. 42). Testes often ovoid, in double layer, often not in middle of segments. Testes number per proglottis (62–70 and 80–90), size (40–55 and 50–70 in diameter) and size of vitellaria (13–16 and 15–33 in diameter) increases between the first 3 cm and after 7 cm

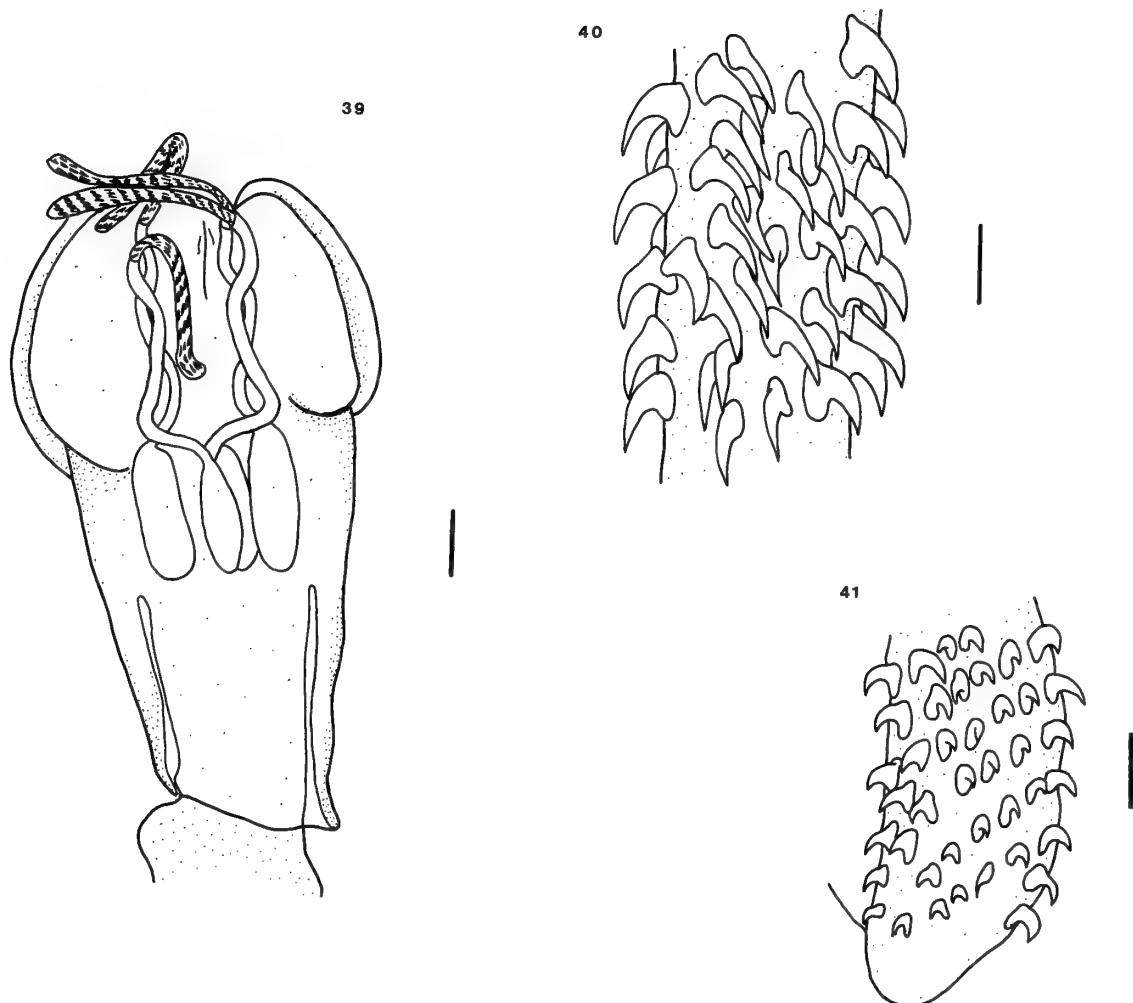


Fig. 39 *Heteronybelinia robusta*. Scolex from *Carcharhinus limbatus*. Scale bar=100 µm.

Fig. 40 *H. robusta* Heteromorphous metabasal armature, bothridial (right hand side) and antibothridial (left hand side) surfaces. Scale bar=10µm.

Fig. 41 *H. robusta*. Heteromorphous basal armature, antibothridial surface. Scale bar=10 µm.

of the strobila respectively. Ovary centally, follicular, with 2 major branches.

REMARKS. The scolex measurements as well as the form and size of the tentacular armature correspond with those in the original description (Dollfus, 1960) and those of specimens from the Mozambique coast (Palm et al., 1997). A high variability in scolex morphology has been described from 20 specimens of 7 host species by Palm et al. (1997). However, *H. yamagutii* is easily distinguishable from all other *Heteronybelinia* species by its metabasal tentacular armature consisting of large claw-like hooks and its basal armature consisting of smaller hooks and characteristic bill hooks. Adult *H. yamagutii* is a large trypanorhynch with segments of different shape and size along the strobila. The testes number as well as the size of testes and vitellaria also vary along the strobila. The present finding is the first report of adult *H. yamagutii*, occurring in *Sphyrna lewini* from South Africa. A world-wide distribution for the species has been proposed by Palm et al. (1997).

Mixonybelinia gen. nov.

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, 4 triangular bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and the scolex. 4 tentacles emerging from bulbs, the retractor muscle originates at the base of the bulbs. 4 proboscides of various length and width, armed with massive hooks; metabasal tentacular armature homeoacanthous with heteromorphous hooks on different tentacle surfaces. Characteristic basal armature consisting of homeomorphous hooks present. Cirrus unarmed, cirrus sac alternates irregularly.

TYPE SPECIES. *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) (subgroup II in Palm et al., 1997).

OTHER SPECIES. *Mixonybelinia southwelli* (Palm & Walter, 1999)

16. *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) comb. nov.

MATERIAL EXAMINED. The Natural History Museum London:

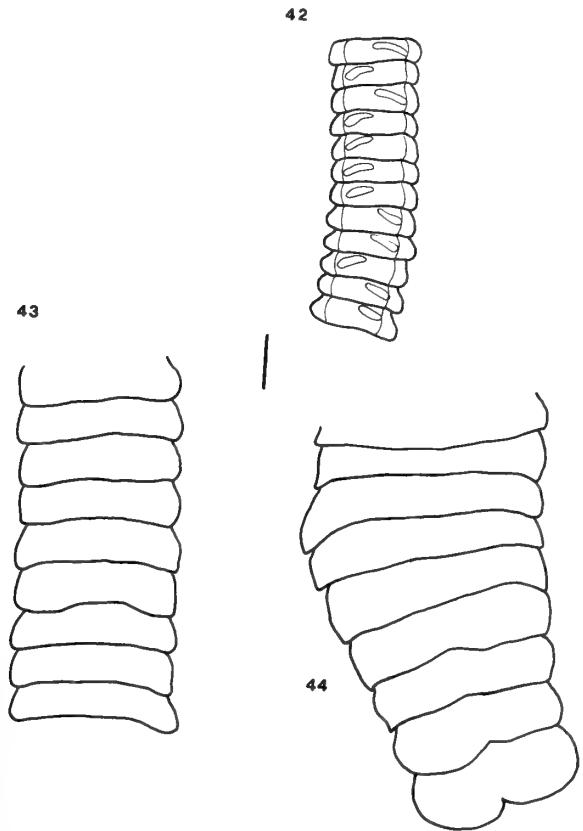


Fig. 42–44 *H. yamagutii*. Strobila 4–5 cm (42) and 7–8 cm (43) behind scolex, and last proglottids (44). Scale bar=500μm.

BMNH 1997.3.24.1, 1997.3.24.2, 1997.3.24.3–4, 1997.3.24.5. *M. beveridgei* was described in detail by Palm *et al.* (1997).

17. *Mixonybelinia southwelli* (Palm & Walter, 1999) comb. nov.

MATERIAL EXAMINED. The Natural History Museum London: BMNH 1977.11.4.7, 1977.11.4.8–9. *M. southwelli* was described in detail by Southwell (1929) and Palm & Walter (1999).

DISCUSSION

Of the material deposited at the British Museum Natural History, 17 different trypanorhynch species, formerly all belonging to the genus *Nybelinia* Poche, 1926, were identified. In addition, two new genera, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov., are erected, and 4 new species, *N. sakanariae* sp. nov., *N. schmidti* sp. nov., *H. heteromorphi* sp. nov., and *H. minima* sp. nov., are described. The new genera separate species with a homeoacanthous, homeomorphous (*Nybelinia*) from those having a homeoacanthous, heteromorphous metabasal armature with heteromorphous basal hooks (*Heteronybelinia* gen. nov.) and from species with a heteromorphous metabasal and homeomorphous basal armature, which are assigned to *Mixonybelinia* gen. nov. *Mixonybelinia* is a tentaculariid genus in which two different armature types occur along the tentacle. This has been described earlier for non-tentaculariid trypanorhynchs, such as the mixodigmatid *Mixodigma*

leptaleum Dailey & Vogelbein, 1982 and the lacistorhynchid *Dasyrhynchus talismani*, Dollfus, 1935 (Dailey & Vogelbein, 1982; Beveridge & Campbell, 1993).

After a first subdivision of the genus by Dollfus (1960), Palm *et al.* (1997) recently subdivided the different *Nybelinia* species on the basis of the tentacular armature and discussed the erection of subgenera. However, the authors did not split the genus into several genera or subgenera. The material in the Natural History Museum clearly demonstrates that the species of the subgroupings as proposed by Palm *et al.* (1997) can be consistently separated on the basis of their characteristic metabasal and basal tentacular armature. They can clearly be recognised, though there is a higher level of intraspecific variation associated with the scolex as well as hook sizes along the tentacles than previously indicated.

Following Campbell & Beveridge (1994) and Palm (1995), the erection of different genera on the basis of the tentacular armature is justified. In their most recent classification, Campbell & Beveridge (1994) used the tentacular armature at the superfamily level, and Palm (1995) at the generic level. In other families within the order, several genera can be distinguished mainly on basis of their characteristic tentacular armature, such as the genera *Callitetrarhynchus*, *Lacistorhynchus*, *Mixodigma*, *Poeciloacanthum* and *Pseudolacistorhynchus* (other examples see Campbell & Beveridge, 1994, Palm, 1995). This simplifies further studies of tentaculariid trypanorhynchs of the *Nybelinia* type.

The present study again demonstrates a high level of morphological variation within different species of *Nybelinia* and *Heteronybelinia*. *Nybelinia africana* and *Heteronybelinia yamagutii* have been re-described and do not correspond in every detail with the original descriptions of the type material. Similar morphological variation occurs in other tentaculariid trypanorhynchs, such as *Tentacularia coryphaenae*, evidenced by the numerous synonymies in the literature (see Dollfus, 1942, Palm, 1995). In comparing the detailed descriptions of 16 *Nybelinia* species recognised by Dollfus (1960), several of them are very similar and can be distinguished only on the basis of minor differences of the hooks, which lie within the limits of intraspecific variation for this character in more recently described species (see Palm & Walter, 1999). Additionally, Palm *et al.* (1997) demonstrated a low host specificity of several *Nybelinia* species, which leads to the suggestion that some of the material examined by Dollfus, which was mainly obtained from the same region off Dakar but from different host fish species, might belong to the same species. This is especially possible in subgroup IIa (*Heteronybelinia estigmene* species complex) and in the *Nybelinia aequidentata* species complex (see remarks above). It is recommended that until the type material and more material from the Dakar region can be examined, the species described by Dollfus (1960) remain valid. However, several are possible synonyms.

Adult tentaculariids also can show a low level of host specificity and different shark species can harbour several *Nybelinia* and *Heteronybelinia* species. During the present study, *Carcharhinus limbatus* and *C. leucas* were found to be infested with 3 species (*Nybelinia scoliodoni*, *Heteronybelinia estigmene*, *H. robusta*) and 2 species (*Nybelinia africana*, *Heteronybelinia estigmene*) respectively. A similar wide host range has been also demonstrated for some other trypanorhynchs (Palm & Overstreet in press, Palm, 1997b) as well as other marine parasite species, such as Antarctic parasites infesting the rock cod *Notothenia coriceps* from the South Shetland Islands (Palm *et al.*, 1998). This behaviour seems to be characteristic for cosmopolitan marine parasitic helminths, such as the nematodes *Contracaecum osculatum* and *Pseudoterranova decipiens*. In conclusion, it is postulated that the currently known tentaculariid genera and most of the species are

characterised by a cosmopolitan distribution pattern, which distinguishes those trypanorhynchs from species such as the eutetrarhynchids of endemic Australian and South American rays (see also Palm *et al.*, 1997, Rego & Dias, 1976). A low level of specialisation of tentaculariids with a flexible, unspecialised life cycle pattern might be essential for these oceanic trypanorhynchs, which would explain for example their occurrence in marine plankton (Dollfus, 1974) as well as the enigmatic infestation of humans (Fripp & Mason, 1983).

The present and previous studies demonstrate that several species exist which change their kind of tentacular armature continuously along the tentacle, such as *N. africana* and *N. lingualis*. Some species change more abrupt between a characteristic basal and metabasal armatures, such as *H. scoliodoni* and *M. southwelli*, while others retain their general hook shape but continuously increase the hook size, such as in *H. estigmene* and *H. robusta*. In *N. aequidentata*, the hook size decreases towards the basal and apical part of the tentacle. It is evident that the tentacular armature within the group is highly variable, making the description of completely evaginated tentacles essential for identification. However, these differences in hook type and size along the tentacles represent an ideal tool for future taxonomic work within these tentaculariid genera.

CLASSIFICATION

The subgroupings of Palm *et al.* (1997) remain a basis for further taxonomic work within tentaculariid trypanorhynchs. Together with the studies of Palm & Walter (1999) (*N. southwelli*) and Jones & Beveridge (1998) (*N. queenslandensis*), 48 species belong to the genera *Nybelinia* (31 species), *Heteronybelinia* (15) and *Mixonybelinia* (2). The current classification of tentaculariid cestodes is as follows:

1. Genus: *Tentacularia* Bosc, 1797

(type and only species: *Tentacularia coryphaenae* Bosc, 1797)

2. Genus *Nybelinia* Poche, 1926 (subgroup I in Palm *et al.*, 1997)

(type species: *Nybelinia lingualis* (Cuvier, 1817))

A Species without characteristic basal armature

a Size of basal hooks smaller than metabasal hooks:

N. aequidentata (Shipley & Hornell, 1906), *N. anthicosum* Heinz & Dailey, 1974, *N. edwinlintoni* Dollfus, 1960, *N. goreensis* Dollfus, 1960, *N. jayapaulazariahi* Reimer, 1980, *N. palliata* (Linton, 1924), *N. queenslandensis* Jones & Beveridge, 1998, *N. riseri* Dollfus, 1960, *N. sakanariae* sp. nov., *N. schmidti* sp. nov., *N. sphyrnae* Yamaguti, 1952, *N. thrysites* Korotaeva, 1971

b Size of basal hooks equal to metabasal hooks

N. anantaramanorum Reimer, 1980, *N. bengalensis* Reimer, 1980, *N. oodes* Dollfus, 1960, *N. pintneri* Yamaguti, 1934, *N. rhynchobatus* Yang Wenchuan, Lin Yuguang, Liu Gencheng & Peng Wenfeng, 1995, *N. strongyla* Dollfus, 1960, *N. surmenicola* Okada, 1929, *N. syngenes* (Pintner, 1929), *N. tenuis* (Linton, 1890), *Nybelinia* sp.

c Size of basal hooks larger than metabasal hooks

N. basimegacantha Carvajal, Campbell & Cornford, 1976

B Species with characteristic basal armature

a Size of basal hooks smaller than or equal to metabasal hooks

N. africana Dollfus, 1960, *N. anguillae* Yamaguti, 1952, *N. bisulcata* (Linton, 1889), *N. erythraea* Dollfus, 1960, *N. indica* Chandra, 1986, *N. lingualis* (Cuvier, 1817), *N. manazo* Yamaguti, 1952, *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharan, 1996)

b Size of basal hooks larger than metabasal hooks

N. gopalai Chandra & Hanumantha Rao, 1985

3. *Heteronybelinia* gen. nov. (subgroup II in Palm *et al.*, 1997)

(type species: *Heteronybelinia estigmene* (Dollfus, 1960))

A Without characteristic basal armature

a Size of basal hooks smaller than metabasal hooks

H. alloiotica (Dollfus, 1960), *H. cadenati* (Dollfus, 1960), *H. elongata* (Shah & Bilquees, 1979), *H. estigmene* (Dollfus, 1960), *H. eureia* (Dollfus, 1960), *H. heteromorphi* sp. nov., *H. karachii* (Khurshid & Bilquees, 1988), *H. minima* sp. nov., *H. punctatissima* (Dollfus, 1960), *H. robusta* (Linton, 1890), *H. senegalensis* (Dollfus, 1960)

b Size of basal hooks equal to or larger than metabasal hooks

H. perideraeus (Shipley & Hornell, 1906)

B With characteristic basal armature

a Size of basal hooks smaller or equal than metabasal hooks

H. nipponica (Yamaguti, 1952), *H. rougetcampanae* (Dollfus, 1960), *H. yamagutii* (Dollfus, 1960)

4. *Mixonybelinia* gen. nov.

(type species: *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997))

Mixonybelinia beveridgei (Palm, Walter, Schwerdtfeger & Reimer, 1997), *M. southwelli* (Palm & Walter, 1999)

5. *Kotorella* Euzet & Radujkovic, 1989

(type and only species: *Kotorella pronosoma* (Stossich, 1901))

Nybelinia lingualis has been considered as belonging to subgroup IAa by Palm *et al.* (1997) and is assigned to subgroup Ba on basis of the gradual change of hook form along the tentacle (see Figs 7–9). The basal hooks without an anterior extension of the base easily distinguish the species from most *Nybelinia*, and therefore are interpreted as a characteristic basal armature. Some other species listed in this classification might change their position after re-examination of the type-material. However, classification as well as comparative discussions on species validity is simplified if using the presented scheme. How strobila morphology such as the shape of segments and structure of the genital complex can be incorporated into this classification will be an important task for future studies.

PHYLOGENY

The above classification most probably does not reflect the phylogeny within tentaculariid trypanorhynchs. Palm *et al.* (1997) failed with their cladistic analysis of the genus *Nybelinia* and the present study

describes in more detail the high morphological variability in hook patterns within the genera *Nybelinia* and *Heteronybelinia*. Although the armature types help in distinguishing between the different species within the group, the same hook forms and patterns are found within *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* species. Beveridge *et al.* (1999) suggested that the transition in armature types from homeoacanthous to heteroacanthous has occurred once and the transition from heteroacanthous to poeciloacanthous types has occurred several times within trypanorhynch evolution. However, it has to be considered that the development of heteromorphous from homeomorphous hook patterns might also have occurred several times within different species, as proposed by Palm (1995). Methods other than morphology will be essential to clarify the phylogenetic situation within the Tentaculariidae.

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A new species of *Microgale* (Lipotyphla, Tenrecidae) from isolated forest in southwestern Madagascar.

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SYNOPSIS. A new species of *Microgale* is described on the basis of two specimens collected in southwestern Madagascar. This species occurs in the Parc National de Zombitse-Vohibasia at 780 m in dry deciduous forest and in the montane habitat of the nearby Analavelona Forest at 1050 m, characterised by a mixture of eastern (humid) and western (dry) plant species. This new species has several distinct cranial modifications that appear to be adaptations for living in areas with semi-xeric conditions. A considerable amount of data is available from southwestern Madagascar on local climatic changes during the Holocene. The biogeography of this new *Microgale* is examined in light of these environmental vicissitudes.

RÉSUMÉ. Une nouvelle espèce de *Microgale* est décrite sur la base de deux spécimens collectés dans le sud-ouest de Madagascar. Cette espèce est présente dans le Parc National de Zombitse-Vohibasi à 780 m dans les forêts sèches caducifoliées ainsi que dans l'habitat montagneux de la Forêt d'Analavelona à 1050 m, dont les plantes sont une composition d'espèces de l'est (humide) et de l'ouest (sèche). Cette nouvelle espèce présente plusieurs modifications crâniennes distinctes qui semblent être le résultat de l'adaptation à des zones de conditions semi-xérophiles. Des données considérables sont disponibles sur la région du sud-ouest de Madagascar sur les changements climatiques durant le Holocène. La biogéographie de ce nouveau *Microgale* est examinée à la lumière de ces vicissitudes environnementales.

INTRODUCTION

When MacPhee (1987) conducted his revision of the shrew-tenrecs belonging to the genus *Microgale*, little recently collected material was available for study and numerous taxa were represented by unique or small series of specimens, often poorly preserved and/or poorly prepared. MacPhee's work utilized the vast majority of material available in the world's natural history museums, which amounted at that time to about 120 specimens. Over the past decade there has been a renaissance in field zoological studies on Madagascar, often in the context of biological inventories, and a considerable amount of new small mammal material has been obtained. For example, the number of recently obtained *Microgale* specimens is many times greater than that available for MacPhee's revision. This new material provides the means to clarify the relationships among some named taxa, a redefinition of species limits, and the description of several new species (Jenkins 1992, 1993; Jenkins *et al.*, 1996, 1997; Goodman and Jenkins, 1998).

During field missions in southwestern Madagascar to the Vohibasia Forest in early 1996 and another to the Analavelona Forest in early 1998 single individuals of a shrew tenrec were captured that, after comparison with the literature and reference collections at several museums, could not be identified to species. Even though the animal is known currently only from two specimens, one of which lacks an associated skull, we feel that its unique pelage and cranial features clearly distinguish it from known taxa and a description is provided below.

MATERIALS AND METHODS

All measurements are in millimeters (mm), with the exception of weight which is in grams (g). Standard external measurements were taken in the field and are defined as follows:

Ear length (E): notch at base of ear to the distalmost edge of the pinna.

Head and body length (HB): tip of the nose to the distalmost point of the body (at base of tail).

Hind foot length (HF): heel to tip of the longest toe (excluding claw). Tail length (TL): base of tail (at right angles to the body) to end of distal-most vertebra, excluding terminal hair tuft.

Weight (Wt): taken with a Pesola spring balance to the nearest 0.5 grams (g).

Cranial measurements were taken using digital calipers or using a microscope measuring stage. Cranial nomenclature follows that of McDowell (1958), Meester (1963) and MacPhee (1981); dental nomenclature that of Mills (1966), Swindler (1976), Butler and Greenwood (1979), and MacPhee (1987). Dental notations are given in the text in the following manner, with premaxillary and maxillary teeth denoted by upper case, mandibular teeth by lower case: incisor (I/i), canine (C/c), premolar (P/p), molar (M/m); thus i3 refers to the third lower incisor.

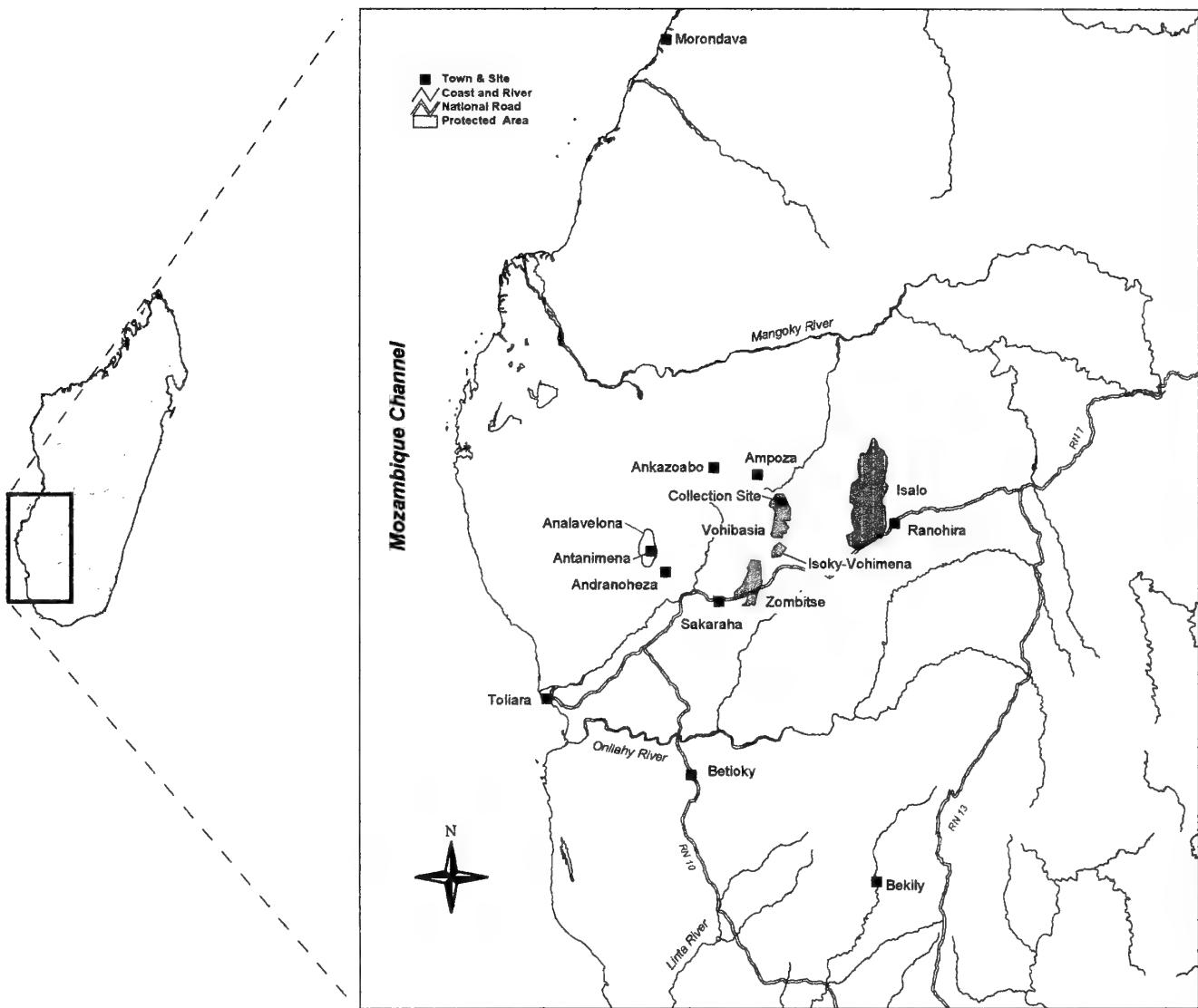


Fig. 1 Map of southwestern Madagascar showing the positions of the Vohibasia and Analavelona forests, as well as other sites mentioned in the text.

RESULTS

Microgale nasoloi sp. nov.

Figs 2–4, 7

HOLOTYPE. FMNH 156187, field number SMG-7875, adult female, skin, skull and skeleton. Collected by S. M. Goodman and R. Rasolosarison on 12 January 1996. The specimen is deposited in the Field Museum of Natural History, Chicago.

TYPE LOCALITY. Vohibasia Forest [Forêt de Vohibasia], 59 km northeast of Sakaraha, Province de Toliara, southwestern Madagascar, 22°27.5'S, 44°50.5'E, 780 m, in transitional dry deciduous forest.

REFERRED MATERIAL. FMNH 161575, field number SMG-10,230,

juvenile male, skin [skull and skeleton lost]. Collected by S. M. Goodman on 14 March 1998 in the Analavelona Forest [Forêt d'Analavelona], near Antanimena, 12.5 km northwest of Andranomeha, 22°40.7'S, 44°11.5'E, 1050 m, on an isolated massif with elements of eastern (humid) and western (deciduous) forests. The specimen is currently at the Field Museum of Natural History and will be repatriated to the Département de Biologie Animale, Université d'Antananarivo, Antananarivo.

DIAGNOSIS. Pelage grey. Interorbital region constricted; braincase shallow; ectotympanic posteriorly positioned; tympanic processes of alisphenoid and basisphenoid reduced. Roots of P2 adpressed; M3 anteroposteriorly compressed, bucco-lingually elongated; p3 scarcely greater in size than p2.

DESCRIPTION. Based on holotype unless otherwise stated. Medium sized *Microgale* (see Table 1), superficially mouse-like in appearance (see Figs 2 and 7), tail thin, well-clothed with long scale

Table 1 Selected dimensions of the holotype and paratype of *Microgale nasoloi* compared with adult specimens of *M. cowani* and *M. brevicaudata*. Data is presented as mean \pm standard deviation, followed by range, with sample size in parentheses.

	<i>M. brevicaudata</i>	<i>M. cowani</i>	<i>M. nasoloi</i> Vohibasia FMNH 156187	<i>M. nasoloi</i> Analavelona FMNH 161575
Character				
HB	75.00 \pm 4.47 66–82 (10)	77.78 \pm 5.64 68–85 (12)	81	70
TL	35.64 \pm 2.84 30–41 (11)	65.44 \pm 3.00 61–71 (11)	53	62
HF	12.55 \pm 0.49 12–13 (11)	16.03 \pm 0.60 15–17 (12)	13	14
E	11.82 \pm 1.11 10–13 (11)	14.19 \pm 1.42 12–17 (12)	16	16
Wt	11.0 \pm 0.89 10–12.5 (6)	13.75 \pm 0.90 12.5–15.5 (8)	14.0	5.9
Condyllo-incisive length	20.87 \pm 0.66 19.9–22.0 (12)	22.38 \pm 0.44 21.4–23.0 (12)	23.2	
Upper toothrow length	9.31 \pm 0.33 8.7–10.0 (12)	10.73 \pm 0.19 10.4–11.0 (12)	10.2	
Rostral breadth	3.53 \pm 0.16 3.3–3.8 (12)	2.47 \pm 0.85 2.3–2.6 (12)	3.1	
Interorbital breadth	5.10 \pm 0.14 4.9–5.4 (12)	5.23 \pm 0.15 5.0–5.6 (12)	4.3	
Braincase breadth	8.83 \pm 0.25 8.5–9.2 (12)	10.07 \pm 0.18 9.8–10.3 (12)	9.2	
Braincase height	5.66 \pm 0.18 5.4–6.1 (12)	6.59 \pm 0.14 6.4–6.8 (12)	4.9	

hairs, shorter than head and body (TL: HB 0.65). Pinnae large and prominent, eyes moderately large. Hindfoot relatively short (HF: HB 0.16). First digit of hindfoot just reaches base of second digit, third digit longest, second and fourth subequal, both slightly longer than fifth. Pelage soft and fine in texture, grey dorsally, grading into darker grey ventrally; manus and pes light buffy grey; lateral portion of rostrum from nose to eyes brown; tail grey, slightly darker above than below, well-clothed with long scale-hairs. Hairs of dorsal pelage grey basally, with pale buffy grey tips, intermixed with guard hairs with grey bases, brown tops and light grey tips. Ventral pelage with grey bases and buffy grey tips. The Analavelona specimen differs slightly in the more pronounced buffy wash on the postero-dorsal and ventral surfaces. Mammary formula: axial 1, abdominal 2, inguinal 1.

Skull medium in length (for dimensions see Table 1) but flattened in appearance and with a narrowly constricted interorbital region (see Fig. 3). Rostrum broad, parallel-sided; interorbital region shallow, long, very narrow and markedly concave; braincase shallow and long, with angular supra-articular facets; lambdoid crest well developed; occipital short, vertically inclined relative to long axis of skull; sinus canal shallowly curved; right and left upper toothrows from I1 to P2 sub-parallel; anterior incisive foramina very large, posterior incisive foramina lie between anterior region of canines; mesopterygoid region long and narrow; mesopterygoid fossa postero-ventrally constricted by markedly inwardly curved pterygoid processes; mandibular fossa broad and shallowly curved; tympanic processes of alisphenoid and basisphenoid very reduced, rostral tympanic process of petrosal reduced; ectotympanic occupies posterior position within tympanic region, not in contact with entoglenoid process of squamosal, tympanic process of alisphenoid or tympanic process of basisphenoid. Mandible moderately robust; coronoid process broad; angular process short and slender but dorsal surface flattened and broad; ascending ramus robust with large dorsal and

ventral articular facets; distance between angular process and ascending ramus short. See Figs 3 and 4 for illustrations of the dentition. First upper incisor (I1) robust, pro-odont, greater in crown height than C, distostyle well developed; short diastema between I1 and I2; I2 robust, approximately equal in crown height to C, anterior accessory cusp and distostyle well developed; I3 small, anteroflexed, slightly taller than distostyle of I2, with which it is in contact; C robust, with small anterior accessory cusp and distostyle; P2 small, slightly greater in crown height than distostyle of C, with which it is in contact, tooth with two closely adpressed roots; P3 small, slightly greater in crown height than I3, protostyle well developed, anterior ectostyle and distostyle present, talon reduced; P4 large, mesostyle, anterior ectostyle and distostyle well developed, talon well developed, especially protocone; well developed, bucco-lingually elongated talons also present on M1 to M3; M3 anteroposteriorly compressed, bucco-lingually elongated. First lower incisor (i1) large, subequal in crown height to i2, hypoconulid (posterior accessory cuspid) well developed; i2 robust, slightly greater in crown height than c, hypoconulid well developed; i3 small, slightly greater in crown height than hypoconulid of i2; c moderately robust, no anterior accessory cuspid, hypoconulid present; p2 small, subequal in crown height to i3, two roots present; p3 small, slightly greater in crown height than p2, with small paraconid and hypoconid; p4, m1 and m2 as in other species of *Microgale*; m3 talonid with low hypoconid, oblique crest and hypoconulid, and shallow talonid basin.

DISTRIBUTION. Known only from the forests of Vohibasia and Analavelona in southwestern Madagascar between 780 and 1050 m (Figure 1).

ETYMOLOGY. This new species is named in honor of the late Nasolo Rakotoarison who was Curator of Mammals at Parc Botanique et Zoologique de Tsimbazaza, Antananarivo. Nasolo was

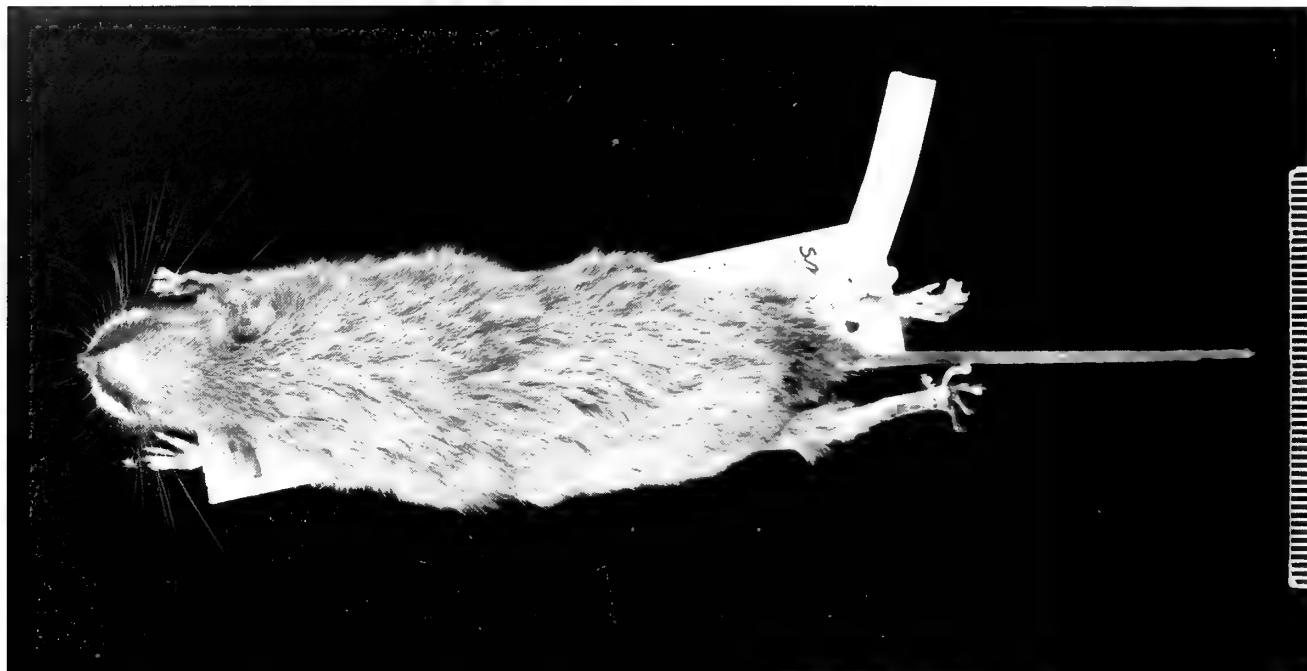


Fig. 2 Dorsal view of skin of *Micogale nasoloi* (FMNH 156187).

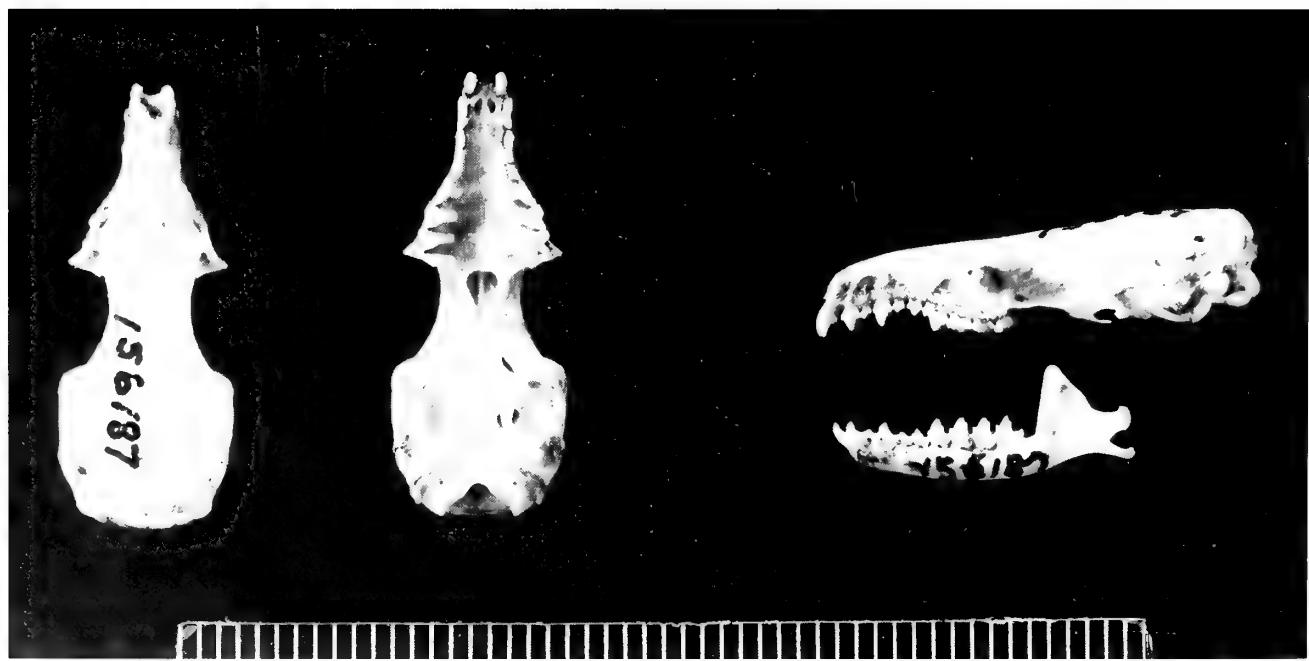


Fig. 3 Dorsal and ventral view of skull, lateral view of skull and mandible of *Micogale nasoloi* (FMNH 156187).

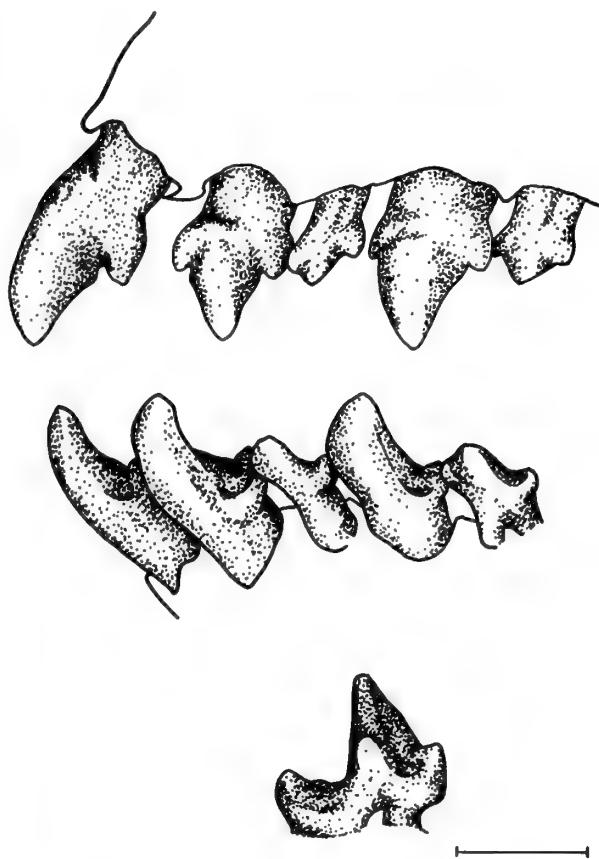


Fig. 4 Dentition of *Microgale nasoloi* (FMNH 156187). Buccal view of left I1 – P2 (above), buccal view of left i1 – p2 (middle), lingual view of left m3 (below). Scale = 1 mm.

passionately interested in mammals and a keen scientist and naturalist.

COMPARISON WITH OTHER SPECIES. Externally *Microgale nasoloi* is readily distinguished from all other species of *Microgale* by the distinctive soft, grey pelage. While it is similar in body size to other medium sized species such as *M. cowani* Thomas, 1882, *M. taiva* Major, 1896a, and *M. drouhardi* G. Grandidier, 1934, larger specimens of *M. fotsifotsy* Jenkins *et al.*, 1997 (for dimensions see Jenkins *et al.*, 1996, 1997) and *M. brevicaudata* G. Grandidier, 1899, the thin, relatively short tail, serves to distinguish it from all of these species with the possible exceptions of *M. brevicaudata* and *M. cowani*. In the case of the latter two species, *M. brevicaudata* has a shorter tail relative to head and body and skull length than *M. nasoloi*, while *M. cowani* has a relatively longer tail (ratio of TL: condylo-incisive length 1.47–1.85 mean 1.70 SD 0.11 n = 10 in *M. brevicaudata*; 2.28 in *M. nasoloi*; 2.7–3.1 mean 3.0 SD 0.13 n = 10 in *M. cowani*).

Microgale nasoloi differs from all other species of *Microgale* in its cranial morphology, particularly the flattened appearance of the skull, in which the shallow braincase is scarcely deeper than the rostrum, the long and very constricted interorbital region and the reduction of some elements of the auditory region. The presence of a well-marked lambdoid crest is a feature shared with *M. brevicaudata* and, to a greater degree, *M. dobsoni* Thomas, 1884 and *M. talazaci* Major, 1896b. The long interorbital region, angular braincase with prominent supra-articular facets and short vertically inclined oc-

ciput of the new species also resembles the condition in *M. dobsoni* and *M. talazaci*.

Microgale nasoloi shows slight similarities in dentition to *M. fotsifotsy* and *M. soricoides* Jenkins, 1993. In *M. nasoloi* I1 is less robust and less pro-odont than that of *M. soricoides*, but more so than in *M. fotsifotsy* and much more so than in other species of *Microgale*; I2 is scarcely smaller than C in *M. nasoloi* and *M. soricoides*; I3 is very small relative to I2 in *M. soricoides*, small in *M. nasoloi* and *M. fotsifotsy*; C is robust but short in crown height as in *M. soricoides*; P2 is small and P3 notably smaller than P4, unlike species of *Microgale* other than *M. dobsoni* and *M. talazaci*. *Microgale nasoloi* differs from other species of *Microgale* in its bucco-lingually elongated talons of P4 to M3, and anteroposteriorly compressed, bucco-lingually elongated M3. Relative sizes of the teeth of the lower anterior dentition are similar to that of *M. fotsifotsy*, with i1 and i2 subequal in crown height and i3 small, unlike *M. soricoides* which has i1 larger than i2.

Preliminary biomolecular analysis provides strong support for a sister relationship between *M. nasoloi* and *M. fotsifotsy* and equally strong support for their sister relationship with *M. soricoides* (Olson, personal communication).

DISCUSSION

Ecology

Vohibasia (15,500 ha) is part of a complex of isolated forest blocks that include Zombitse (14,200 ha) and several smaller satellite forests (see Fig. 1; these surface area estimates are based on 1991 aerial photographs (Langrand and Goodman, 1997). These forests are floristically transitional between eastern humid forest and western dry deciduous forest (Morat, 1973; Du Puy *et al.*, 1994), yet structurally they are closer to dry deciduous forest than humid forest (Fig. 5). Other than these isolated fragments, which were once contiguous, little remains of this transitional forest habitat in southwestern Madagascar, largely as a result of clearing and burning forest for cattle pasture (Salomon, 1993). In 1998, these two forest blocks and the smaller satellite site of the Isoky-Vohimena Forest, were declared as a new reserve known as the Parc National (PN) de Zombitse-Vohibasia.

The Vohibasia Forest generally has a relatively dense understorey, that may at least in part be the result of regeneration after selective removal of hardwoods a few decades ago. Average tree height is less than 10 m (Pétignat *et al.*, 1997). In general the woody vegetation is not particularly spiny in comparison to sub-arid thorn scrub (spiny bush) slightly further west and south. The soils are fine alluvial sands from the Isalo Formation, surface water is highly seasonal, and there is generally little or no soil humus.

The vertebrate communities inhabiting the Zombitse-Vohibasia forests are apparently typical of those found in other arid regions. The known small mammal community consists of five tenrecid lipotyphlans (*Tenrec ecaudatus* Schreber, 1778, *Setifer setosus* (Schreber, 1778), *Echinops telfairi* Martin, 1838, *Microgale nasoloi* and *Geogale aurita* Milne Edwards & G. Grandidier, 1872), one soricid (*Suncus madagascariensis* [Coquerel, 1848]), two exotic murine rodents (*Rattus rattus* [Linnaeus, 1758] and *Mus musculus* Linnaeus, 1758) and two nesomyine rodents (*Eliurus myoxinus* Milne Edwards, 1885 and *Macrotarsomys bastardi* Milne Edwards & G. Grandidier, 1898) (Goodman & Ganzhorn, 1994; Goodman & Rasoloarison, 1997).

To the west of the Zombitse-Vohibasia Forest, a region characterised by a dry climate and distinct deciduous vegetation, is the



Fig. 5 View down old road in the Vohibasia Forest that was cut for geological exploration. Note the relatively dense understorey and sandy soils lacking leaf litter or humus. The trapping site of *Microgale nasoloi* was to the right and about 10 m into the forest. (Photograph by S. M. Goodman).

isolated mountain of Analavelona rising to over 1300 m (FTM, 1979). On the basis of earlier botanical classifications, Humbert & Cours Darne (1965) described the upper zone of the Analavelona Forest as low sclerophyllous forest ('Forêt basse sclérophylle'), surrounding areas of low-lying forests to the east (e.g. Zombitse-Vohibasia) as dry dense forest ('forêt dense sèche') and to the west as Didiereaceae and *Euphorbia* bush ('Didièreacées et Euphorbia haut fourré'). The nearest low sclerophyllous forest to the Analavelona Massif is in the Isalo range, about 110 km to the east. Thus, according to this classification the massif holds a different flora from the immediately surrounding forests.

On the eastern side of the Analavelona Massif the foothills start at about 600 m, and the lower limit of the forest is at about 1000 m and runs to the upper reaches of the mountain. On the basis of botanical research conducted in this forest by Nathalie Messmer and Pierre Jules Rakotomalaza during the March 1998 expedition to the site, in the lower altitudinal portion of the forest massive emergent *Ficus* and *Eugenia* trees with diameter at breast height of 95–110 cm reach heights of up to 25 m. The generic composition of these forest trees indicate that the site is a mixture of eastern humid and western deciduous forest. Considerable ground humus and leaf litter and some epiphytic plants are present, the understorey is open and small streams drain the steep hills. These characteristics are unlike sclerophyllous forest, therefore the classification presented by Humbert & Cours Darne (1965) for Analavelona is inaccurate, although it is possible that the final summatal ridge of the mountain is dominated by sclerophyllous plants. On the basis of numerous phytological characteristics the portion of the forest that we visited

is much closer to Humbert & Cours Darne's mid-elevation humid forest ('types humides, moyenne altitude (800–1300 m)'). In summary, the forested portion of the Analavelona Massif is heterogeneous with regards to vegetative structure, particularly differences between the western and eastern slopes (Koechlin *et al.*, 1974).

The Analavelona Massif is distinctly moister than any other region of southwestern Madagascar that we are aware of, including portions of the Isalo Massif. Presumably on the basis of orographic position, Analavelona receives regular and considerable precipitation and even during the dry season the summatal zone is often shrouded in mist. The extant fauna and flora contain elements that indicate that this site may be a refuge for biota that had much more extensive distributions in southwestern Madagascar when this region was moister in the relatively recent geological past (Raxworthy and Nussbaum, 1997; Goodman, unpublished). The known small mammal community of Analavelona is relatively depauperate and consists of three tenrecid lipotyphlans (*Tenrec ecaudatus*, *Echinos telfairi* and *Microgale nasoloi*), one soricid (*Suncus madagascariensis*), one introduced murine rodent (*Rattus rattus*) and one nesomyine rodent (*Eliurus myoxinus*) (Goodman, unpublished).

Trapping

Generally on Madagascar, pit-fall buckets have produced good results in capturing ground-dwelling vertebrates, particularly reptiles, amphibians, and lipotyphlans (Raxworthy & Nussbaum, 1994; Goodman *et al.*, 1996). During the April 1993 mission to the Zombitse Forest 528 pit-fall bucket days were amassed; in January 1996 in the Vohibasia Forest, 165 pit-fall bucket days; and in March

1998 in the Analavelona Forest, 198 pit-fall bucket days (Raxworthy *et al.*, 1994; Goodman & Rasoloarison, 1997; Goodman, unpublished). During the same periods, a combination of Sherman and National Live traps were used for a total of 1,088 trap nights in the Zombitse Forest, 955 trap nights in the Vohibasia Forest, and 535 trap nights in the Analavelona Forest. The only individual of *M. nasoloi* taken in one of these devices in the Vohibasia Forest was in a Sherman Live trap baited with a mixture of peanut butter and ground corn flour placed about 1.5 m off the ground, and set about 10 m into the forest from the edge of an old road surrounded by forest habitat. The single individual of this species obtained in the Analavelona Forest was in a pit-fall device placed within 25 m of the forest edge. Given the general efficiency of these two trapping techniques in capturing a wide variety of non-volant small mammals, including terrestrial and semi-arboreal lipotyphlans, it appears that *M. nasoloi* is uncommon or difficult to trap with these devices.

Presumably this species also occurs in at least the nearby Zombitse Forest and perhaps other smaller forest satellites that until their recent fragmentation were part of an extensive area of transitional forest. It was not found in the Isoky-Vohimena Forest (22°41.0'S, 44°49.8'E), lying between Zombitse and the PN de l'Isalo which was inventoried in late January 1996.

Natural history

The lipotyphlan fauna of Madagascar is much more diverse in humid areas of the island and only a few species have been recorded in the drier west and southwest. Other than those species mentioned above for the Zombitse-Vohibasia and Analavelona forests, three others have been reported in dry areas of the island. *Microgale brevicaudata* is known from the northwest possibly as far south as Morondava or Toliara (MacPhee, 1987; Raxworthy & Nussbaum, 1994; Ganzhorn *et al.*, 1996); *M. pusilla* Major, 1896a from the Mahafaly Plateau in the extreme southwest, although this material recovered from owl pellets may date from a period in recent geological times when this region was more mesic (MacPhee, 1986); and a long-tailed *Microgale* associated with the *longicaudata* group from near Morondava (Ade, 1996).

Little biological data may be gleaned from the capture of the two individuals of *M. nasoloi*. The Vohibasia animal was a pregnant female with two embryos in the left and one in the right oviduct; the embryos measuring 10 mm in crown to rump length. On the basis of embryo size, the female was near parturition at the time of capture in mid-January. In contrast to the data available for species of *Microgale* recorded from eastern humid forest, no quantitative information on the reproductive season of small lipotyphlans is available from the southwestern portion of the island. Nevertheless, given that in the eastern humid forest a considerable number of *Microgale* species give birth during the early portion of the rainy season, which normally commences in late November and early December, a mid-January date for parturition would coincide with the beginning of the rainy season in southwestern Madagascar which tends to occur later than in the east (Donque, 1975).

The individual from Analavelona was a male with small abdominal testes measuring 3 × 2 mm and non-convoluted epididymides. Unfortunately, the skull is not available to assess the age of the individual using dental characters, but on the basis of reproductive condition this animal was probably a juvenile. Further evidence to support this supposition is that the male is smaller than the adult female in several external measurements and body mass, all characters that tend to vary with age. The pit-fall bucket in which the male was captured contained the chewed remnants of beetles and cockroaches, which it presumably fed upon before being removed from

the trap.

The Vohibasia specimen was trapped 1.5 m above the ground on a vine running from the soil surface to the mid-canopy at an angle of about 15° (Fig. 6), suggesting that it must be at least competent at scrambling along supports. Anatomically however, it does not exhibit the features normally associated with arboreality in other members of the genus, since the relatively short tail and hindfoot suggest a greater affinity for a mainly terrestrial lifestyle. In the most extreme cases, *M. longicaudata* Thomas, 1882 and *M. principula* Thomas, 1926 have very long, naked-tipped tails approximately twice as long as head and body length, long hindfeet, and are demonstrably able to make use of slender supports above the ground (Goodman & Jenkins, 1998). Caution should be exercised in attributing morphological adaptations to particular lifestyles, since *Echinops*, which lacks an external tail is nevertheless an adept climber.

The thesis expounded by Eisenberg & Gould (1970), that species of *Microgale* may be divided into different locomotory classes based on differences in tail and hindfoot length relative to head and body length, was criticised by MacPhee (1987) because of lack of ecological evidence. Recent direct observation, plus mainly circumstantial evidence from trap locations, suggest that many species of *Microgale* are generalists equally at home on the ground as scrambling amongst lower levels of the understorey; while a few also use additional ecological niches, such as the long-tailed *M. longicaudata* and *M. principula* which are adept at exploiting thinner supports above ground level.

Microgale nasoloi exhibits some features – pale pelage, prominent pinnae, short hindfoot relative to head and body length, skull with a broad bimaxillary region, narrow interorbital constriction, flat and broad braincase with pronounced superior articular facets and marked lambdoid crest, well developed anterior dentition and anteroposteriorly compressed M3 – which in combination are unique to this species of *Microgale*. Many of these features are, however, also present in the Malagasy geogaline tenrec, *Geogale aurita*, while several are reminiscent of the suite of external, cranial and dental characters which Hutterer (1986) used to define *Afrosorex* as a subgenus of *Crocidura* (Lipotyphla: Soricidae). Species assigned to *Afrosorex* inhabit savanna or forest-fringe areas and the pale dorsal pelage coloration and prominent pinnae, shown also by *Geogale* and *M. nasoloi*, are presumably adaptations to semi-xeric conditions. The parallelism in dental features is possibly also an example of similarities in dietary adaptations. One of the other three species of *Microgale* known to occur in dry habitats is *M. brevicaudata*, and this species also shows some features converging on *M. nasoloi*, *Geogale* and *Afrosorex*. Externally all of these taxa have prominent ears and short hindfeet, while all but *M. nasoloi* have a markedly short tail, however *M. brevicaudata* shows none of the craniodental features shared by *M. nasoloi*, *Geogale*, and *Afrosorex*. This suggests that these shared external features are more plastic than the cranial features and are thus more readily influenced by the dry conditions of savanna or forest fringe habitats, or that species such as *M. brevicaudata* have been adapting to dry or to less extreme conditions for a shorter evolutionary period than others such as *M. nasoloi* and *Geogale*.

Biogeography

Just a few kilometers from the Vohibasia Forest there is the paleontological site of Ampoza, which has yielded a remarkable amount of subfossil material that provides insight into environmental change in southwestern Madagascar over the past few millennia. On the basis of current data derived from a pollen core at Andolonomby (75 km SW from Analavelona and 140 km SW from



Fig. 6 Exact position of trap in the Vohibasia Forest that captured the holotype specimen of *Microgale nasoloi*. The trap was placed about 1.5 m off the ground and the trap opening was facing the direction of the canopy and it is most likely that the animal was descending the vine when captured. Note the thick woody understorey of the forest. (Photograph by S. M. Goodman).

Vohibasia), these climatic shifts involved a mesic period starting before 5000 years Before Present (BP) and an arid period between 3500 and 2500 years BP (Burney, 1993). These proposed shifts are mirrored in changes of species representation and habitat types of subfossils excavated from sites in southwestern Madagascar (Goodman & Rakotozafy, 1997) including Ampoza (Goodman, in press). Radiocarbon dates available from Ampoza include an AMS date of 1350 ± 60 BP from a bone of *Hypogeomys antimena* A. Grandidier, 1869, an endemic large rodent that no longer occurs in the region (Goodman & Rakotondravony, 1996). Further, bone remains of extinct giant tortoises from the site have been dated to 1910 ± 120 BP (Mahé & Sordat, 1972) and 2035 ± 35 BP (Burleigh & Arnold, 1986). Although these radiocarbon dates are more recent than Burney's proposed period of aridification, the important point for this discussion is that over the past few millennia there has been significant change in the environment of the Vohibasia and Analavelona region as reflected by the fauna.

Over the past few years a number of studies have tried to correlate aspects of the speciation of certain Malagasy vertebrates with vicariant events derived from information on shifts in vegetational



Fig. 7 Photograph of the live individual of the holotype of *Microgale nasoloi* (FMNH 156187). (Photograph by J. Durbin).

communities during the Quaternary. These paleoecological extrapolations are derived almost exclusively from palynological data dating from the Holocene. In many cases several of the hypotheses advanced seem to explain patterns of the distribution of certain taxa, particularly those living in montane zones of the east (Carleton & Goodman, 1996, 1998). A similar argument in the case of *Microgale nasoloi* may be formulated as follows: during the recent geological past when the region was more mesic, the distinctly more humid forest currently restricted to the upper reaches of the Analavelona Massif would have been more extensive, consequently, *M. nasoloi* would have had a broader distribution. As the climate became drier and the humid forest retreated towards the summits of the Analavelona, the distribution of this animal also contracted, leaving remnant populations at sites with suitable habitat to support it, such as the Vohibasia Forest.

For *M. nasoloi* there appears to be a conflict between aspects of morphological adaptations, namely a species adapted to semi-xeric conditions and the above scenario associated with a more mesic Holocene in southwestern Madagascar. Given these adaptations it is possible that the opposite sequence took place – as more mesic forest dominated the landscape this species was pushed into drier areas of the southwestern Madagascar, and only after becoming more arid was it able to colonize or recolonize this region. On the basis of very limited information it appears that this species is forest-dwelling and

currently restricted to the forests of Analavelona and Vohibasia. However no intensive small mammal surveys, particularly with pitfall traps, have been conducted in spiny bush areas of southwestern Madagascar or the PN de l'Isalo and this species might have a much broader distribution than currently known. Analavelona is a form of mist-oasis and almost certainly a Pleistocene (or earlier) refuge for humid forest-dwelling animals (Raxworthy & Nussbaum, 1997), while the Vohibasia Forest shows transitional aspects between the humid forests of the east and the deciduous forests of the west. Given the ecological variation in this region during the Holocene and recent times, a single coherent explanation for the distribution of this species is not obvious. It exists in the most mesic portions of southwestern Madagascar and is unknown from spiny bush. Perhaps during historical periods when there was more forest cover in the region its distribution was more widespread.

In recent years several studies have examined the phylogeny of reputed Malagasy vertebrate adaptive radiations, often using biochemical characters. Using models of genetic clocks these studies indicate that much of the mammalian intrageneric speciation took place during the Pliocene (Jansa *et al.*, in press). No information is available on the paleoecology of southwestern Madagascar dating from the Pliocene and most of the Pleistocene. If indeed the period in which *Microgale nasoloi* speciated falls within this same epoch and was the result of some vicariant event such as a shift in vegetational structure, we are currently unable to propose models to put its modern distribution into any geographical context.

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Modes of ear reduction in iguanian lizards (Reptilia, Iguania); different paths to similar ends

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Synopsis. New observations are presented on interspecific variation in ear structure in *Phrynocephalus* (Agamidae) and the Chamaeleonidae. The tympanum has probably been obscured at least fourteen times in the Iguania and more extensive ear reduction has occurred independently at least once in each of five separate clades. Combining information on ear reduction with estimated phylogenies of the groups concerned demonstrates that the process has been initiated in at least two quite different ways in the Iguania. Modifications to the ear are congruent with hypotheses of phylogeny based on other characters in *Tympanocryptis*, the *Cophotis-Lyriocephalus-Ceratophora* clade, phrynosomatid sand lizards, and to a large extent in the Chamaeleonidae. In *Phrynocephalus* there is evidence that some modifications show partial reversal in one or more lineages.

INTRODUCTION

Different lineages of organisms often evolve a number of similar traits independently, but the order in which these are assembled may often be different, even in ecological analogues, especially if the taxa concerned are not closely related (Arnold, 1994). This phenomenon of equipotentiality, where more or less the same overall condition is reached by different routes, will be demonstrated in the external and middle ear of iguanian lizards, using some new anatomical observations and recent information on the phylogeny of this assemblage. Reduction of the external and middle ears can be shown to have occurred a number of times but by at least two primary initial routes, the various changes making up the process taking place in different sequences.

Versluys (1898) and Mertens (1971) listed cases where the tympanum is obscured in the Iguania and more extensive ear reduction in the group has been surveyed by Smith (1938). More recently, Wever (1978) discussed selected instances of ear modification in greater detail and gave information on the ability of such altered organs to transmit sound. The present account corrects some errors in Smith's otherwise useful paper and describes the wide variety of previously unreported ear conditions found in the genus *Phrynocephalus* and some more modest differences among chameleons.

MATERIAL EXAMINED

Material examined forms part of the collection of the Natural History Museum, London and a list of specimens checked is deposited in the Reptile Section there.

NOMENCLATURE

Various changes in iguanian nomenclature have been suggested recently and, to avoid confusion, usage in this paper will be specified here. The use of Phrynosomatidae for what were previously informally called sceloporine iguanids (Savage, 1958), which has been

put forward by Frost and Etheridge (1989), is accepted. On the other hand, these authors' use of Chamaeleonidae is not followed. They employ the name for the whole of the Acrodonta, which comprises Chamaeleonidae in its usual sense plus what has generally been called Agamidae, including the Uromastycidae (Borsuk-Bialynicka & Moody, 1984).

Moody (1980) allocated the wide range of lizards which had long usually been referred to the genus *Agama* to a number of separate genera: *Stellio*, *Agama*, *Xenagama*, *Pseudotrapelus* and *Trapelus*. This course was followed by several authors, but the name *Stellio* is unavailable (Stejneger, 1933) and the group it was used to denote by Moody is paraphyletic, comprising distinct Palaearctic and mainly African assemblages (Joger, 1991) of which the former is probably a clade and the members of the latter more closely related to such taxa as *Agama*, *Pseudotrapelus* and *Trapelus* (personal observations). Leviton, Anderson, Adler & Minton (1992) argue for the use of *Laudakia* Gray, 1845 for the Palaearctic forms, a course followed here. The more recent suggestion (Henle, 1995), that *Laudakia* should be confined to some members of this assemblage and the rest placed in *Placoderma* Blyth, 1854, requires more thorough assessment of the relationships of these lizards. The name *Acanthocercus* Fitzinger, 1843 is available for the remainder of the forms that Moody allocated to *Stellio* (see Schätti & Gasperetti, 1994; Henle, 1995; Baig & Böhme, 1997).

DISTRIBUTION OF EAR REDUCTION IN THE IGUANIA

Basic structure of the unreduced Iguanian middle ear is shown in Fig. 1. In extreme cases of reduction, the tympanic area is covered by the anterior slip of the *depressor mandibulae*, the tympanum itself is absent and the columella becomes more robust. The distal part of the extracolumella may virtually disappear while at the same time its attachments to surrounding structures are thickened and sometimes ossified. These attachments are the internal or quadrate process, connecting to the lower quadrate bone, and the dorsal process which may connect to the paroccipital process, the intercalary ligament, or both.

At least some reduction of the ear occurs within the following apparently holophyletic groups of the Iguania.

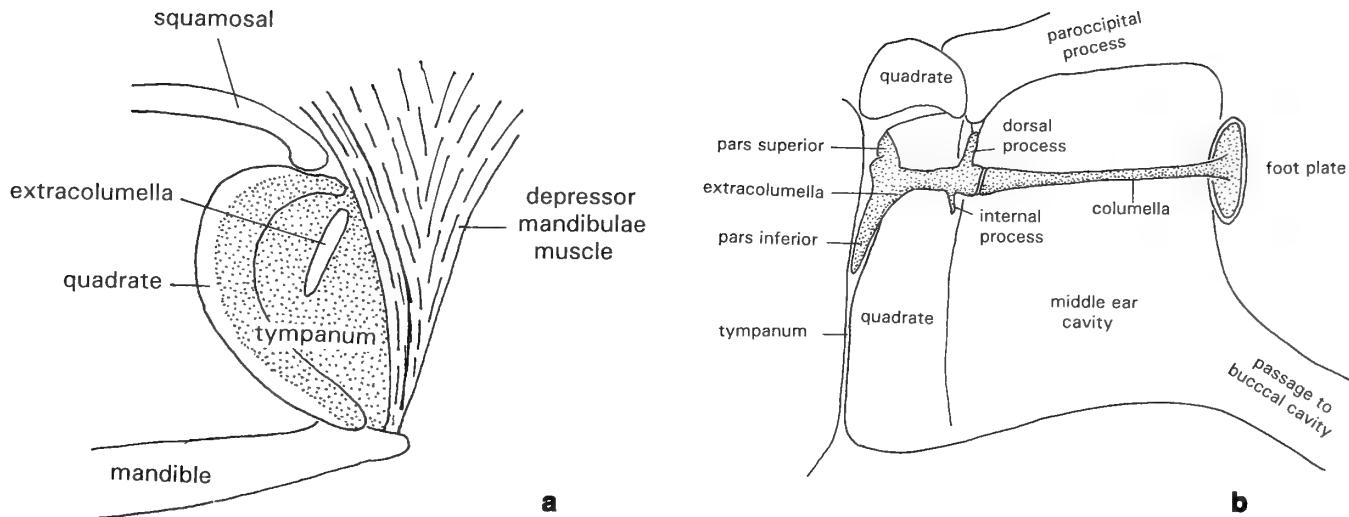


Fig. 1 General structure of the ear in Iguania. a. Lateral view of left ear, tympanum stippled. b. Transverse section of left ear. Figures based on those of Baird (1970).

Australian agamids

(Fig. 2)

Among Australian agamids of Group 3 (Moody, 1980), ear modification has occurred independently in *Ctenophorus maculosus* (Mitchell, 1948) and in all the species of *Tymanocryptis* Peters, 1863, except *T. adelaidensis* and *T. diemensis* (data from Cogger, 1992). In *Ctenophorus maculosus* and the *Tymanocryptis parviceps* Storr, 1964 group the ear is covered with scaly skin but the tympanum is present just beneath it (Greer, 1989). In the *Tymanocryptis lineata* group (species examined: *T. lineata* Peters, 1863, *T. intima* Mitchell, 1948 and *T. cephalus* Günther, 1867) further reduction has occurred. The anterior slip of the *m. depressor mandibulae*, has moved forwards beneath the skin to cover the tympanic area, the columella is more robust, no clear tympanum exists, the extracolumella is reduced to a small projection, and the dorsal and internal processes are robust and sometimes ossified. The middle ear opens broadly into the buccal cavity in *T. lineata* and *T. intima*, but more narrowly in *T. cephalus*.

Arboreal agamids of the Oriental region

(Fig. 2)

Among mainly arboreal agamids of the Oriental region which constitute Group 4 (Moody, 1980), a fully exposed tympanum is lacking in some or all members of the following apparent clades (relationships based on the weighted and unweighted Wagner tree analyses of Moody, 1980) 1. *Gonocephalus* Kaup, 1805 (partly obscured in *G. miotympanum* (Günther, 1872)); 2. *Japalura* Gray, 1853 (some species); 3. *Phoxophrys* Hubrecht, 1881; 4. *Otocryptis* Wagler, 1830; 5. *Draco* Linnaeus, 1758 (some species); 6. *Ptycholaemus* Peters, 1864; 7. *Aphionotis* Peters, 1864, *Ceratophora* Gray, 1834, *Cophotis* Peters, 1861 and *Lyriocephalus* Merrem, 1820; and 8. *Oriocalotes* Günther, 1864 (some individuals).

The tympanum consequently may have become obscured at least eight times in the Oriental assemblage (although *Phoxophrys* and

Otocryptis could represent a single origin if reversal occurred in *Sitana*, the apparent sister group of the latter genus). In groups where members vary in the degree to which the tympanum is obscured, such as *Draco*, *Japalura* and *Oriocalotes*, it is apparent that covering of the external ear has taken place by development of scales on the tympanic surface (Fig. 5). Although most of the Oriental taxa with hidden tympana lack the extensive modifications found in some *Tymanocryptis*, there may be less extreme changes. *Draco* for instance has a thick columella, the stem of the extracolumella is angled relative to this, and the air-filled space in the middle ear is restricted; there is also a substantial loss of sensitivity (Wever, 1978).

Only in the clade made up of *Aphaniotis*, *Cophotis*, *Lyriocephalus* and *Ceratophora* has the process of ear modification gone further. The relationships of this group (based on Moody, 1980) are shown in Fig. 2. In this assemblage, the basal *Aphionotis* has the tympanum covered (Fig. 5c), but little other change is apparent, apart from the columella being robust and the exposure of the extracolumella on the tympanum large (checked in *A. acutirostris* Modigliani, 1889, *A. fusca* (Peters, 1864) and *A. ornata* Lidth de Jeude, 1893). In the sister genera *Cophotis* and *Lyriocephalus*, the tympanum has disappeared and this area is covered by the anterior slip of the *m. depressor mandibulae*. The pars superior of the extracolumella is absent, the pars inferior is small and projects laterally, and the dorsal and internal processes are robust and ossified, the former attaching substantially to the paroccipital process. The quadrata itself is more or less straight and without an auditory cup, while the middle ear cavity extends laterally as far as the tympanic area and has a quite large opening to the buccal cavity. In *Ceratophora*, the ear is essentially similar (illustrated by Wever, 1978) but there are no openings from the buccal cavity to a distinct middle ear cavity (checked on *C. aspera* Günther, 1864, *C. stoddarti* Gray, 1834 and *C. tennentii* Günther, 1861).

Smith (1938) erroneously attributed a highly modified middle ear structure to *Aphaniotis* and also incorrectly described the middle ear openings to the buccal cavity of this genus, *Cophotis* and *Lyriocephalus* as being strongly reduced.

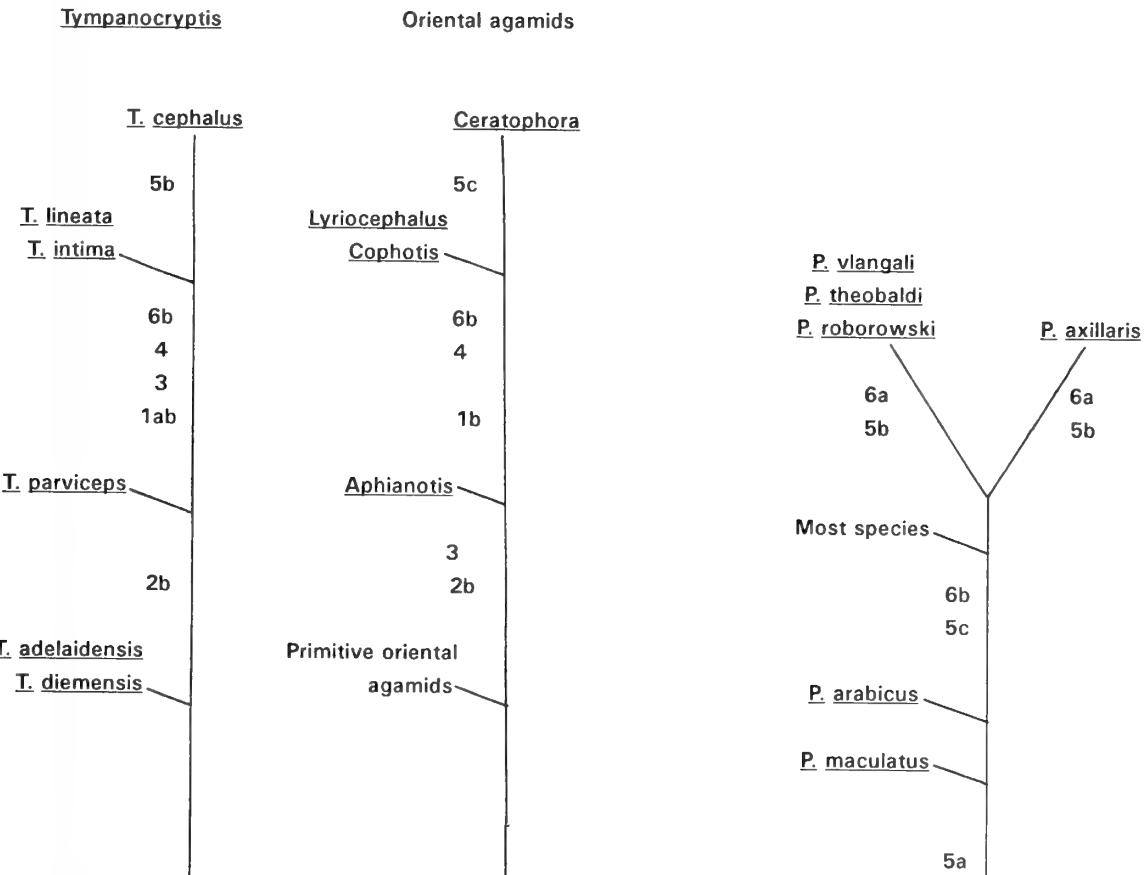


Fig. 2 Pattern of ear reduction in *Tympanocryptis* (Agamidae), and in the clade made up of *Aphianotis*, *Lyriocephalus*, *Cophotis* and *Ceratophora* (Agamidae).

Abbreviations: 1. depressor mandibulae moves forwards, a - slightly, b - extensively. 2. Tympanum covered, largely - a, entirely - b; 3. columella robust. 4. tympanum disappears. 5. buccal opening to the middle ear reduced, a - somewhat, b - strongly, c - very small or absent. 6. Pars inferior of extracolumella reduced, a - somewhat, b - strongly or absent.

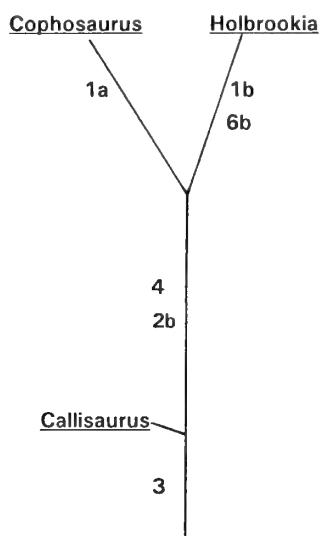


Fig. 4 Pattern of ear reduction in phrynosomatid sand lizards (Phrynosomatidae). For abbreviations see Fig. 2.

Fig. 3 Pattern of ear reduction in *Phrynocephalus* and its relatives (Agamidae). For abbreviations see Fig. 2.

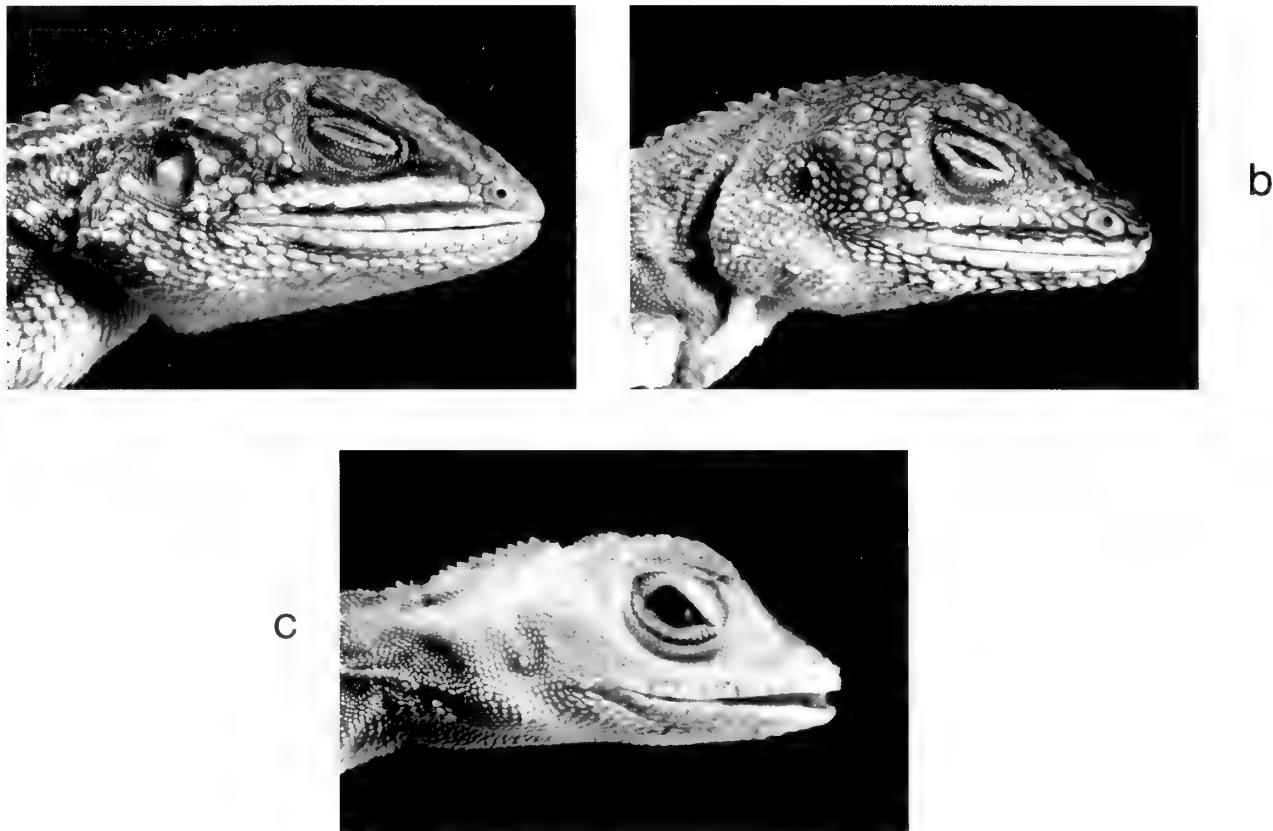


Fig. 5 Stages in reduction of the external ear in Oriental agamids. a. Tympanum superficial and exposed, *Japalura dyomondi*, BMNH 1914.3.2.2.; tympanum indicated by a depression but covered with scales, *Japalura polygonata ishikagiensis*, BMNH 1913.3.10.9; tympanic area scarcely sunk and covered with unmodified skin, *Aphaniotis fusca*, BMNH 1886.12.28.12–13.

Phrynocephalus and its relatives

(Fig. 3)

Moody (1980), on the basis of his morphological study of the Agamidae, regarded *Phrynocephalus* as the sister group of *Laudakia* plus *Acanthocercus* and a relationship to *Laudakia* has also been supported by immunological evidence (Joger, 1991). However, a more detailed anatomical investigation (in progress) suggests that *Phrynocephalus* is the sister group of *Bufoniceps* Arnold, 1992 (a new generic allocation for *Phrynocephalus laungwalaensis* Sharma, 1978) and successively more distant relatives are *Trapelus*, *Pseudotrapelus*, various African taxa the relationships of which are yet to be fully resolved including *Agama*, *Xenagama* and species assigned to *Acanthocercus*, and then *Laudakia* (Fig. 3). This hypothesis of relationships is used in the following reconstruction of the history of ear reduction in the group. However, even if *Phrynocephalus* plus *Bufoniceps* is regarded as the sister group of *Laudakia*, only evidence for the initial changes in stage 1 below would be lost.

An estimate of *Phrynocephalus* phylogeny based on morphology (Arnold, 1999) suggests that successive branches on the main lineage are: *P. mystaceus*; *P. maculatus*; *P. arabicus*; the *P. interscalparius* group (*P. interscalparius*, *P. sogdianus*, *P. ornatus*, *P. clarkorum*, *P. luteoguttatus* and *P. euptilopus*); *P. scutellatus*; *P. golubevi*; *P. reticulatus*; *P. raddei*; there is then a large clade made up

of most of the remaining species. Within the latter assemblage, little robust phylogenetic structure is apparent but *P. roborowski*, *P. theobaldi* and *P. vlangali* are clearly closely related to each other and perhaps more distantly to *P. forsythi*.

1. In some *Trapelus*, the anterior slip of the *m. depressor mandibulae* moves anteriorly to partly obscure the tympanum, producing a short meatus with a small opening (Fig. 6b; at the same time the bar-like, superficial part of the extracolumella becomes more horizontal).
2. In *Bufoniceps*, the tympanum is directed more posteriorly, the *m. depressor mandibulae* moves further forward and the meatus and its surface opening become very narrow (Fig. 6c), so that its depth is several times the width of the latter.
3. In all *Phrynocephalus*, the tympanic area is entirely covered by skin (Fig. 6d) and substantially by the *m. depressor mandibulae*. In *P. mystaceus*, there is still a well defined tympanum incorporating an extracolumella which lacks the pars superior, but the pars inferior is large and overlaps the conch of the quadrate. The dorsal process is long and joins the intercalary cartilage, and the internal process is quite slender. The buccal opening to the middle ear is large and extends from the back of the basisphenoid process well beyond the spheno-occipital tubercle of the basi-occipital bone; its greatest dimension is over 25% of the head length in small specimens.



Fig. 6 Stages in reduction of external ear in the clade containing *Phrynocephalus*. a. Tympanum superficial and fully exposed, *Pseudotrapelus sinaitus* (BMNH 1953.1.7.9); b. tympanum sunk and external opening of meatus so formed reduced, *Trapelus agilis* (BMNH 94.11.13.4); c. tympanum deeply sunk and meatus and external opening very narrow, *Bufocephalus laungwalaensis* (BMNH 1975.1592); d. meatus totally closed *Phrynocephalus maculatus* (BMNH 1973.2038).

4. In *P. maculatus* the tympanum is reduced to a delicate membrane and, while smaller than in *P. mystaceus*, the extracolumella still overlies the quadrate; the buccal opening to the middle ear is reduced in size, its greatest dimension being about 15–20% of the head length. *P. arabicus* is similar but the buccal opening is rather smaller.
5. In most of the other species of *Phrynocephalus* which form a large terminal clade, the extracolumella is very small or absent and, if present, does not overlap the quadrate or only slightly. The buccal opening to the middle ear is also minute or absent.
6. The only exceptions to this arrangement within the large terminal clade of *Phrynocephalus* are *P. robowski*, *P. theobaldi*, *P. vlangali* and *P. axillaris*. These are generally similar to *P. maculatus* and *P. arabicus*, but the entrance to the middle ear is smaller, not extending beyond the spheno-occipital tubercle of the basi-occipital bone, the greatest dimension being about 10–14% of the head length. Relationships within *Phrynocephalus* suggest that the condition found in these species results from evolutionary reversal with the extracolumella increasing in size and the buccal entrance of the middle ear re-evolving or at least enlarging. Reversal may have occurred twice: in the common ancestor of the first three species and perhaps independently in *P. axillaris*.

Some variation also exists within *Phrynocephalus* in the extent to which the anterior slip of the *m. depressor mandibulae* extends over

the quadrate bone and whether the dorsal and internal processes are ossified, although this does not constitute a regular phylogenetic pattern.

Chameleons

In chameleons, the skin over the quadrate region is more or less like that covering surrounding areas, the tympanum has disappeared and the *m. depressor mandibulae* runs close to the quadrate which is straight; the columella is short, and the extracolumella elongate, with a superior ligament attached to it.

Variation exists, for instance in the form of the pars inferior of the extracolumella and the extent to which this is embedded in the *m. depressor mandibulae* (Wever, 1968). There is an anterior process extending to the flattened posterior section of the pterygoid in *Chamaeleo quilenis* Bocage, 1866. *C. senegalensis* Daudin, 1802 and *C. chamaeleon* (Linnaeus, 1758) (Wever, 1978) and in *C. dilepis* Leach, 1819 and *Bradyopodium ventrale* (Gray, 1845) (personal observations). This is lacking in *Chamaeleo ellioti* Günther, 1895, *C. fischeri tavetanus* Steindachner, 1891, *C. hoehnelii* Steindachner, 1891 and *C. jacksoni* Boulenger, 1896 (Wever, 1968), in the Madagascan *C. brevicornis* Günther, 1879 and *C. lateralis* Gray, 1831 (referred to *Calumna* Gray, 1865 and *Furcifer* Fitzinger, 1843 respectively by Klaver & Böhme, 1986), and in the dwarf *Rhampholeon brevicaudata* (Matschie, 1892) and *Brookesia stumpffi* Böttger, 1894 (personal observations).

Among the same species, the African forms assigned to *Chamaeleo* Laurenti, 1763 have small but well developed buccal openings into the middle ear, but these are less obvious although present in the two large Madagascan forms examined. In *Bradypodion ventrale* there are indentations where the openings would normally be but the openings themselves are absent. This is also true of the *Rhampholeon* Günther, 1874 and *Brookesia* Gray 1865 studied in which there are not even indentations.

Ear reduction in the Phrynosomatidae

(Fig. 4)

Relationships within the Phrynosomatidae are discussed by De Queiroz (1992) and ear structure of various members of the group is described by Earle (1961a, b, c; 1962), Wever (1978) and Montanucci (1987).

In *Phrynosoma* there is stiff skin over the tympanum and sometimes this is very like that surrounding it, but middle ear structure is basically normal. *Uma* has an essentially unmodified ear, but in *Callisaurus* the columella is more robust and contacts the inner edge of the quadrate bone, while the extracolumella is more heavily built, directed backwards and has much stronger dorsal and internal processes; the quadrate is also somewhat modified. In *Holbrookia* and *Cophosaurus*, there is no ear opening, the tympanum is absent and the columella is even more robust attaching to the quadrate via a short, broad internal process. *Cophosaurus* has the tympanic area partly covered by the *m. depressor mandibulae* and the quadrate is more or less straight instead of cup-shaped. In *Holbrookia*, the extracolumella is very reduced, covering of the tympanum by muscles is greater than in *Cophosaurus* but modification of the quadrate rather less.

PATTERNS OF MODIFICATION

In summary, a limited degree of external and middle ear reduction, including covering of the tympanum by unmodified skin, has probably occurred at least fourteen times in the Iguania. More extensive modification has taken place in *Tymanocryptis*, the *Cophotis-Lyriocephalus-Ceratophora* clade, *Phrynocephalus*, the Chamaeleonidae and the *Callisaurus-Holbrookia-Cophosaurus* clade. In all these groups, different species exhibit markedly different degrees of modification. When these varied conditions are plotted on phylogenies of the groups concerned (Figs 2–4), it is possible to get some idea of the order in which particular features of the modified ears appeared. To be able to reconstruct a complete sequence on a lineage, the origin of each new feature must be separated from those of others by side-branches, otherwise, reconstruction will be impossible or incomplete (Arnold, 1994). In the Chamaeleonidae only two basic degrees of modification exist and only three in *Tymanocryptis*, in *Aphaniotis-Cophotis-Lyriocephalus-Ceratophora*, and in *Callisaurus-Holbrookia-Cophosaurus*. In the clade containing *Phrynocephalus*, on the other hand, there are at least six successive conditions.

It is apparent that the sequence of ear modification has been different in some groups even though the end results have substantial similarity. Thus, in the Oriental agamids, and *Ctenophorus* and *Tymanocryptis*, the tympanum was first obscured by becoming scaly (Fig. 5) and only then did other changes take place, such as the *m. depressor mandibulae* moving forwards to cover the tympanic area and the columella becoming more robust. In contrast, more

basal members of the clade containing *Phrynocephalus* show that movement of the *depressor mandibulae* muscle took place first, creating and then narrowing a meatus (Fig. 6) and it was only when this process was complete that the tympanum was entirely cut off from external contact. In phrynosomatids, the earliest change involved the columella and extracolumella becoming more robust, rather than the tympanum becoming obscured. Complete closure of the buccal opening is the final stage in the groups where it occurs but, in the *Callisaurus-Holbrookia-Cophosaurus* clade, has not taken place, even though the ear is otherwise highly modified.

The reasons for the extensive ear modification found in some iguanians are uncertain. The ground-dwelling forms that exhibit these conditions occur in arid areas and many of them burrow directly into loose sand or earth. In this situation, covering or modifying the primitively delicate tympanum and associated middle ear structures may protect them from damage. Again, a more robust columella with direct attachment to the quadrate may be more efficient at transmitting low amplitude vibrations generated on or in the substrate by predators, prey or conspecifics. Ability to detect such vibrations sometimes has clear benefits, for instance in the sand-burrowing *Scincus scincus* (Hetherington, 1989). However these possible performance advantages seem unlikely to apply to the various tree dwelling forms that exhibit reduction of the external and middle ears. It might be expected that the differences, in the order in which specific modifications of the ear appear, result from different selective regimes or different sequences of these. However, differences in order of modification even occur between ground-dwelling forms, in which selective regimes are likely to be similar.

USE OF THE OUTER AND MIDDLE EARS IN THE SYSTEMATICS OF THE IGUANIA

Although loss and reduction features are often said to be of low value in phylogeny reconstruction (see for instance Hecht and Edwards, 1977), changes in the outer and middle ear of the Iguania do not always fit this preconception. Obscuring of the tympanum has occurred many times, but loss of more structure is often congruent with changes in other characters within groups. Thus ear alterations do not conflict with phylogenies based on other features in *Tymanocryptis*, the *Aphaniotis-Cophotis-Lyriocephalus-Ceratophora* clade and in the phrynosomatid sand-lizard group. Similarly, there is some congruence with classifications of chameleons based on lung and hemipenial structure (Klaver & Böhme, 1986). For instance within *Chamaeleo* the development of a pterygoid connection to the columella is confined to the subgenus *Chamaeleo*. However, loss of a buccal opening to the middle ear occurs in the *Brookesia-Rhampholeon* group but is also found in *Bradypodion* which may be more closely related to other larger chameleons (Klaver & Böhme, 1986). Although many changes in the ear on the *Phrynocephalus* lineage are congruent with the phylogeny, this group is exceptional in showing reversal in some ear features.

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Symbols in text. Male and female symbols within the text should be flagged within curly brackets to enable setter to do a swift global search.

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